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USING STABLE ISOTOPES TO ASSESS THE TROPHIC ECOLOGY OF A NATIVE AND
INVASIVE FISH SPECIES IN THE WESTERN BASIN OF LAKE ERIE

by

Matthew M. Guzzo

A Thesis
Submitted to the Faculty of Graduate Studies
through the Great Lakes Institute for Environmental Research
in Partial Fulfillment of the Requirements for
the Degree of Master of Science at the
University of Windsor

Windsor, Ontario, Canada

2010

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ISBN: 978-0-494-80236-6
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Chapter 2	Guzzo, M.M, G.D. Haffner, S. Sorge, S.A. Rush & A.T. Fisk. Spatial and temporal variability of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ within lower trophic levels of a large lake: Implications for estimating the trophic relationships of consumers.	Manuscript submitted to Hydrobiologia: November, 2010.
Chapter 3	Guzzo, M.M, G.D. Haffner, S. Sorge, S.A. Rush & A.T. Fisk. Resource utilization and niche overlap of a native and invasive fish species in the western basin of Lake Erie.	Manuscript to be submitted to Biological Invasions.

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ABSTRACT

Using stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), I investigate the trophic ecology and niche overlap of Yellow Perch (*Perca flavescens*) and White Perch (*Morone americana*) across the western basin of Lake Erie. Stable isotopes varied spatially and temporally in lower trophic level organisms, which are used to estimate carbon sources and trophic position of consumers. These variations inhibit our ability to assess trophic relationships, particularly in large lakes. Yellow Perch relied on benthic food sources, while White Perch occupied higher trophic positions and had larger niche widths. Trophic positions of yellow and white perch were related to size however a lack of $\delta^{13}\text{C}$ - length relationship suggests these species exhibit no changes in carbon source. Significant differences in $\delta^{13}\text{C}$ / $\delta^{15}\text{N}$ and high niche overlap among Yellow and White Perch indicated that the species are utilizing different forage bases, however, have the potential to compete if resources become limited.

DEDICATION

I dedicated this thesis to my parents, Rita and Terry, who have supported me in all my life endeavours. Without you, this would not have been possible.

ACKNOWLEDGEMENTS

I would like to thank the Canadian Research Chair Program for funding; Sandra Ellis, Anna Hussey, Kristen Diemer, Mary-Lyn Maillieux, Eric Primeau and Carly Ziter for their help in the lab; Stuart Sorge for help in the field; Scott Rush for statistical help; Aaron and Doug for their insights and contributions to this work.

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CHAPTER 1

GENERAL INTRODUCTION

Thesis introduction

Ecology is the interdisciplinary study of species distribution, abundance and the relationships of organisms to one another and the environment. To fully understand the interaction of species, we must examine the feeding relationships of species. This specific area of ecology has become known as food web ecology and is one of the more central and unifying concepts in ecology (Lindeman, 1942; Martinez, 1995). It is used to quantify processes such as species interactions, contaminant transfer and ecosystem stability. Food webs are also becoming an important component of managing fish stocks using an ecosystem approach, which is particularly important to freshwater fisheries due to increased disruptions related to aquatic invasive species.

As the science of food web ecology has evolved, the scale of research projects and questions have become larger and more complicated and classic food web techniques, such as stomach contents, have limited advancement. The use of chemical tracers, such as stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) have become increasingly popular to study the structure and dynamics of food-webs (Vander Zanden & Rasmussen, 1996; Post, 2002). While widely-used, there has been little work describing the limitations brought about by spatial and temporal variability of stable isotopes within habitats of large lakes.

This thesis examines the relative carbon sources and trophic positions of a native and invasive fish species across the western basin of Lake Erie using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Lake Erie is home to the second largest freshwater fishery in the world and has a valuable recreational fishery, but there are concerns about its fish stocks. However, before this could goal could be

addressed, I first quantified, in chapter 2, the isotope variability in lower trophic level species such as young-of-year fish and examined the implications of this variability on estimating trophic position of young-of-year fish using sessile, baseline organisms such as Zebra Mussels (*Dreissena polymorpha*). The results of chapter 1 were then used to inform and guide the interpretation of stable isotopes data for Yellow (*Perca flavescens*) and White Perch (*Morone americana*) that addresses the carbon sources and trophic positions of fish in Lake Erie (chapter 3).

Food web ecology

Food webs represent the feeding relationships between species within an ecosystem. The concept of food web diagrams were originally the idea of Pierce et al. (1912) and later Shelford (1913) who illustrated ‘food cycles’ which included food chain linkages between consumers and prey and were defined as collections of food chains dependent upon a primary food source (photosynthesis). The food web concept was further developed in the 1927 publication *Animal Ecology* (Elton, 1927), in which Elton introduced his ‘pyramid of numbers’, where he stated that animals at the base of the food web would be in high in diversity and biomass, while those at the top would be low in diversity and biomass. Although the concept of food cycles and the pyramid of numbers were breakthroughs in the field of ecology, they were based on biomass and trophic levels and lacked a currency to which interactions among organisms could be evaluated.

The work of Lindeman (1942) recognized that both all life and function within ecosystems was dependant on the movement of energy as a result of feeding interactions between organisms, referred to as ‘trophic dynamics’. In addition to the idea of trophic dynamics, ‘trophic linkages’ refer to the feeding interactions among species and are necessary in tracing energy flow through ecosystems (Cohen & Briand, 1984). Initially, food webs were

constructed by grouping members in an ecosystem into a sequential series of discrete trophic levels, called 'food chains'. The height of these food chains were limited by energy transfer between trophic levels where by trophic level one (primary producers) would provide all necessary energy for trophic level two (primary consumers), with trophic level two providing all necessary energy to trophic level three, and so on (Elton, 1927; Lindeman, 1942; Hairston & Hairston, 1993). The use of discrete trophic levels failed to incorporate complexity and omnivory that characterizes natural systems (Polis & Strong, 1996; Vander Zanden & Rasmussen, 1996; Persson, 1999) which led to the use of fractional trophic levels (Odum & Heald, 1975) or estimates of trophic position (Vander Zanden et al., 1997) which allowed a more quantitative incorporation of these species into food chains.

In contrast to food chains, classical food web studies used species lists along with the presence or absence of feeding links and relied on the ability of investigators to estimate trophic position of organisms in the field. These food web studies captured the complexity of trophic interactions in ecological communities, but were time-consuming to construct, often subjective in their resolution and scope (Paine 1988), and did not weigh feeding links according to their energetic or functional importance, making them ineffective in tracing energy and mass flow through ecosystems (Polis, 1991; Hairston & Hairston, 1993; Polis & Strong, 1996; Persson, 1999; Vander Zanden & Rasmussen, 1996). Classic food web studies were also hindered by migrating species and the ability to collect the requisite quantitative dietary data for all species interacting in food webs (Vander Zanden & Rasmussen, 1999).

Stable isotopes in food web ecology

Stable isotopes, particularly those of carbon and nitrogen have become popular tool in evaluating the structure and dynamics of food webs (Peterson & Fry, 1987; Kling et al., 1992;

France, 1995; Vander Zanden et al., 1999; Post et al., 2000) and allow for the use of both the trophic level and food web concepts in food web ecology (Post, 2002). Unlike stomach contents, which provide a “snapshot” view and are susceptible to empty stomachs, digested prey, and require large sample sizes (Bootsma et al., 1996; Grey et al., 2001), stable isotopes capture both omnivory and track energy and mass through ecosystems by providing time-integrated view on an organisms feeding behavior (Peterson & Fry, 1987; Kling et al., 1992; Cabana and Rasmussen, 1996).

Most elements exist in multiple forms called isotopes, which have the same number of protons and electrons, but vary in the number of neutrons contained within the nucleus and as a result form similar bonds and compounds (Peterson & Fry, 1987). Isotopes can be either radioactive, in which excess neutrons are given off by the nucleus over time in order to become more stable (same number of protons and neutrons); or stable, where extra neutrons persist within the nucleus. Stable isotopes of an element are classified as either ‘heavy’ (e.g., ^{15}N) or ‘light’ (e.g., ^{14}N) depending on their atomic mass (neutron + protons); the heavier isotope is usually found in lower concentrations in nature. The relative proportions of these stable isotopes often vary across the environment, which gives these isotopes unique tracer capabilities (Peterson & Fry, 1987). Biologically induced changes in relative stable isotope abundances are due to their variable kinetics and result in ‘fractionation’- a change in relative isotope concentration of two stable isotopes proportional to the difference between their masses (Schmidt, 2003). Stable isotopes are most often presented in δ -notation, the percent difference of heavy to light isotope relative to a reference standard, calculated as

$$\delta X = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000,$$

where X is the heavier isotope (e.g., ^{13}C), R_{sample} is the raw ratio of heavy to light isotope in the sample and R_{standard} is the raw ratio of heavy to light isotope in an internationally accepted standard. These standards are PeeDee Belemnite for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$. Variation in relative isotope abundances often occurs at very low concentrations and thus stable isotope ratios are expressed 'per mille' (‰) as the multiplication by 1000 makes changes more obvious (Jardine et al., 2006).

The stable isotope approach is based on the principle that the stable isotope ratios in the tissues of consumers can be related in a predictive way to those in their diet (DeNiro and Epstein, 1978; 1981). Stable carbon isotopes ratios have little ($\sim 1\text{‰}$) or no change in the relative abundance of ^{13}C between trophic levels following consumption of a primary producer by primary consumers (Hobson & Welch, 1992). This quality allows $\delta^{13}\text{C}$ to be used to determine sources of primary productivity in systems where two or more isotopically distinct sources exist (e.g., benthic vs. pelagic) (Hobson et al., 1995). Stable carbon isotope ratios often vary between primary productivity sources: C^3 versus C^4 photosynthesis; inshore versus offshore in aquatic systems; and pelagic versus benthic in aquatic systems (France, 1995). This difference between C_3 and C_4 photosynthesis is C_4 plants do not lose CO_2 during photosynthesis and thus are enriched in ^{13}C (Forsberg et al., 1993). Differences between inshore and benthic/pelagic sources is presumed to result from a boundary layer surrounding benthic algae and macrophytes, which decreases the diffusion rate of CO_2 compared to pelagic algae. As a result, benthic algae and macrophytes are often forced to use all available CO_2 that results in very little change in $\delta^{13}\text{C}$ while pelagic algae are not limited by CO_2 diffusion and will preferential use ^{12}C - CO_2 , resulting in a lower $\delta^{13}\text{C}$ (Peterson & Fry, 1987; France, 1995). Therefore, benthic algae will have a have a higher $\delta^{13}\text{C}$ value, which will, in turn, be reflected in the consumers that feed on it.

Values of $\delta^{15}\text{N}$ of consumers become enriched in ^{15}N relative their prey, more so than $\delta^{13}\text{C}$, and therefore serve as a measure of trophic position, particularly in aquatic systems (DeNiro & Epstein, 1981). In general, nitrogen isotopes are typically discriminated against in a common magnitude among animals as they feed and digest food and therefore provide useful information on trophic level and food web structure (Minagawa & Wada, 1984). During the digestion and assimilation of food, consumers preferential select and catabolize amino acids containing the light nitrogen isotope (^{14}N), making them enriched in ^{15}N relative to their diet (Minagawa & Wada, 1984). This resulting difference in stable isotope ratios between an organism and its food (ie. $\delta^{15}\text{N}_{\text{predator}} - \delta^{15}\text{N}_{\text{prey}}$) is called a diet-tissue discrimination factor and are typically 3-4‰ for $\delta^{15}\text{N}$ in aquatic food webs (DeNiro & Epstein, 1981; Minagawa & Wada, 1984; Post, 2002). Using diet-tissue discrimination factors and $\delta^{15}\text{N}$ values the trophic position (TP) of various members of an ecosystem can be estimated using the equation:

$$\text{TP} = [(\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{baseline}}) / \Delta^{15}\text{N}] + \text{baseline TP},$$

where $\delta^{15}\text{N}_{\text{fish}}$ represents the $\delta^{15}\text{N}$ value of the organism being estimated for, $\delta^{15}\text{N}_{\text{baseline}}$ represents the $\delta^{15}\text{N}$ value of species with known trophic position and $\Delta^{15}\text{N}$ denotes an increase in $\delta^{15}\text{N}$ (typically 3.4‰) for one trophic level (Jardine et al., 2006).

Although widely used, there are several caveats surrounding the application of stable isotopes to food web studies (Gannes et al., 1997; del Rio et al., 2009; Wolf et al., 2009). For example, when estimating trophic position with stable isotopes the calculation must include the $\delta^{15}\text{N}$ value of an organism of known trophic position which captures both spatial and temporal variation of energy sources values so that changes in trophic position reflect variation food web structure and carbon flow (Post, 2002; Jardine, 2006). Trophic position estimates also rely on the assumption that $\delta^{15}\text{N}$ values have diet discrimination factors ranging 3-4 ‰, for each trophic

level (DeNiro & Epstein, 1981; Minagawa & Wada 1984; Post 2002) and studies often select these diet-discrimination factors to distinguish trophic levels based on published reviews. This remains a concern as these values have been shown to vary across species, temperature, tissue type and diet (Post, 2002; Frazer et al., 1997; Hobson & Clark, 1992; Caut et al., 2009). Another uncertainty surrounding the use of stable isotopes in food web studies is that stable isotopes can vary spatially and temporally in single aquatic ecosystems (Syvaranta et al., 2006; Mbabazi et al., 2010; Zambrano et al., 2010). While previous studies have accounted for this variability in stable isotopes at the base of the food web across multiple systems (e.g., Hebert et al., 1999), the variability of stable isotopes of lower trophic level species within single habitats type of a large lake has received little attention. These species are often used to baseline trophic position calculations and provide a forage base for larger predatory fish. Therefore, variation in stable isotopes of these lower trophic level organisms could potentially inhibit our ability to assess trophic relationships among consumers.

Study system

The research for this M.Sc. was implemented in the western basin of Lake Erie (Fig. 1.1), a shallow (average depth 7.5 m, maximum depth 19 m), flat basin that comprises the western third of this most southerly Great Lake. The basin is classified as mesotrophic and experiences vertical mixing with limited summer stratification (Kane et al., 2009). Spatial complexity in the western basin of Lake Erie is produced via tributary and connecting channel hydraulic inputs, most notably the Detroit and Maumee Rivers. Although the Detroit River contributes significantly more total water flow into the system than the Maumee, ~80% to ~5% respectively, the Maumee River contributes ~ 35% of the total phosphorous load to the basin (Baker & Richards, 2002, Dolan & McGunagle, 2005) and provides warm nutrient rich waters which

circulate in the southwest portion of the lake relative to the Detroit River, which provides a much larger flow of cooler nutrient poorer waters (Reichert et al., 2010). Both rivers also vary in their spatial and seasonal subsidies of nutrients and energy and contribute to environmental heterogeneity with respect to water temperatures, plankton communities, production dynamics and fish assemblages in the basin (Barbiero et al., 2001a; Barbiero et al., 2001b; Reichert et al., 2010).

Rationale

Laurentian Great Lakes food webs have recently seen major shifts in species assemblages, which presumably have changed trophic relationships (Hebert et al., 1999). Forage fish stocks have collapsed and predatory fish are experiencing decreases in their growth potential and energy densities (Roy, 2004; Paterson, 2005). Despite these major changes, the food web of the western basin of Lake Erie have not yet exhibited the major trophic collapses as reported in food webs of other Great Lakes (Guinand et al., 2003; Lumb et al., 2007; Paterson et al., 2009). The western basin of Lake Erie's diverse forage base makes it one of the most resilient food webs (Regier & Hartman, 1973) in the Great Lakes system and although western Lake Erie has been shown to be energy rich, there is evidence for limitation. The basin supports an intensive commercial and sport fishing industry which has been shown to account for up to 53% of the total annual primary production in the system, more than 6 times the recommended 8% of primary production required to sustain fisheries (Pauly & Christensen, 1995; Fitzpatrick et al., 2008). Invasive species also pose a threat to limiting resource availability in the basin. Stoeckmann & Garton (1997) concluded that exotic Zebra Mussels potentially consume 10-50% of summer primary production in the western basin.

This potential for resource limitation highlights the importance for understanding the resource utilization of fish species within the western basin of Lake Erie. Yellow Perch make up a large proportion of Lake Erie commercial catches, however recently there has been concern about their population in the basin (Yellow Perch Task Group, 2010). While these declines could be a result of increased fishing pressure, it may also be to do resource overlap with an invasive species, the white perch. As larvae, both species are heavily dependent on plankton, until they undergo an ontogenetic shift where they become demersal and begin to feed on benthos. Adult Yellow Perch and White Perch typically range from 15.0 – 30.0 cm and 12.0 – 18.0 cm respectively and are opportunistic feeders (Parrish & Margraf, 1990; Mittelbach & Persson, 1998). Diet studies indicate that both species feed heavily on abundant benthos in spring, zooplankton blooms in summer and move to piscivory in late summer when prey fish become abundant (Parrish & Margraf 1994; Morrison et al., 1997). Despite their similar feeding strategies, morphological differences, particularly the more up-turned mouth of White Perch allows this species to be more efficient in planktivorous feeding. As a result, zooplankton has been found in White Perch stomachs throughout the season, even when alternative prey items are in abundance suggesting a more opportunistic feeding strategy of White Perch relative to Yellow Perch (Schaeffer and Margraf, 1986; Parrish & Margraf, 1990).

While some studies have suggested that allochthonous sources of energy may be a greater contributor to the western basin food web than previously acknowledged (Leach, 1975), this contribution has yet not been quantified. If allochthonous sources do account for a large proportion of production in the basin, I predict that spatial and temporal variability of stable isotope values in lower trophic level organisms will exist due to differences in land use around

the lake and seasonality. Additionally, assuming that the intense fishing pressure and invasive species are resulting in a resource limited environment, I predict that as opportunistic feeders, Yellow and White Perch will have significant resource-use overlap in the western basin of Lake Erie.

Objectives

1. Quantify the extent of spatial and temporal variability in stable isotopes of lower trophic level species in the offshore habitat of the western basin of Lake Erie and its potential impact on estimating the trophic position of secondary consumers.
2. Examine the resource utilization and niche overlap of Yellow Perch and White Perch across sites of varying nutrient availability the western basin of Lake Erie using stable isotopes.

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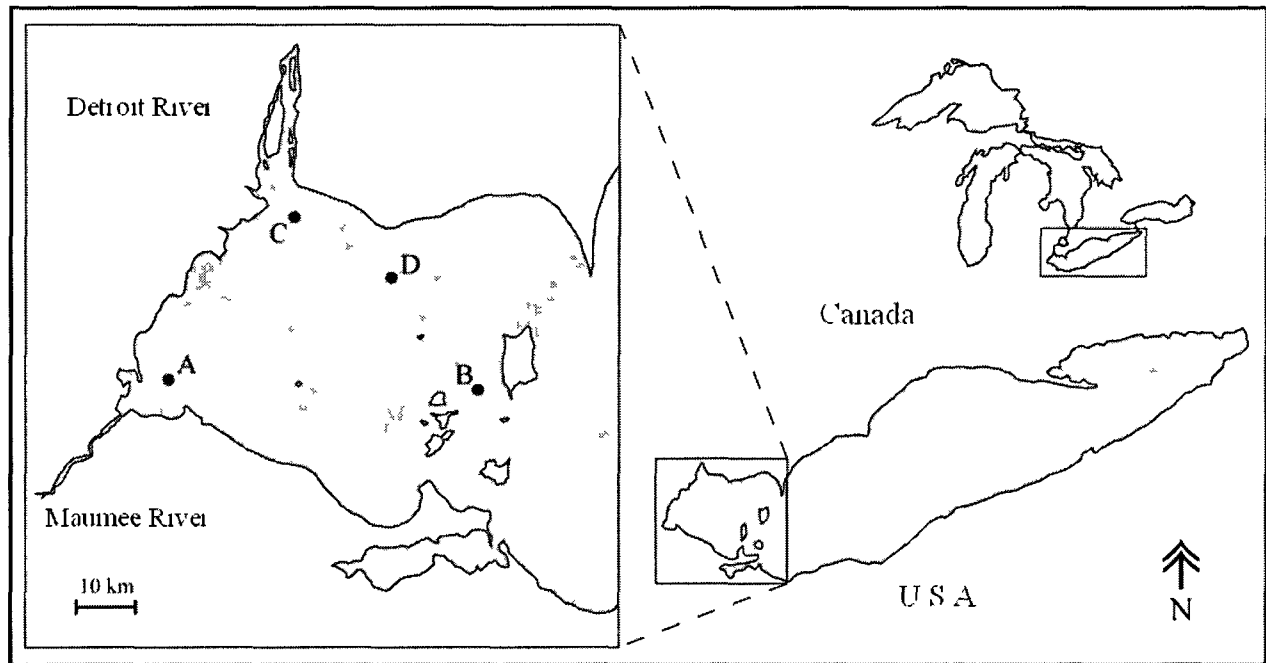


Figure 1.1 Location of sampling sites in the western basin of Lake Erie, sampled during June-September 2009. Letters A-D represents fixed sampling site. A= Maumee River Plume, B= Bass Islands, C= Detroit River Plume, D= Middle Sister Island.

CHAPTER 2

SPATIAL AND TEMPORAL VARIABILITY OF $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ WITHIN LOWER TROPHIC LEVELS OF A LARGE LAKE: IMPLICATIONS FOR ESTIMATING THE TROPHIC RELATIONSHIPS OF CONSUMERS

Introduction

Food webs represent energy and nutrient flows within an ecosystem and have long been a central theme in ecology (Lindeman, 1942; Martinez, 1995). The study of food webs provides insight into species interactions and enhances the understanding of the processes that structure ecosystems (Vander Zanden & Rasmussen, 1996; Hobson et al., 2002; Post, 2002). One of the most common tools used for studying the structure and energy flow within food webs are stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$). Stable isotopes of carbon can provide insight into the sources of primary producers in aquatic food webs, and in lakes are often used to differentiate between littoral (nearshore)/benthic and pelagic (open water) primary production (Peterson and Fry, 1987; France, 1995; France and Peters, 1997). Stable isotopes of nitrogen provide a means to quantify the trophic position (TP) of organisms, where consumers become enriched in ^{15}N relative to their prey by an average of 3.4‰ for $\delta^{15}\text{N}$ providing a space and time integrated measure of TP (Minagawa & Wada, 1984; Peterson & Fry, 1987, Cabana & Rasmussen 1994). In order to overcome across-system variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, carbon sources and TPs are often normalized to the stable isotope values of a common primary consumer, such as unionid mussels to represent baseline values of pelagic and littoral food webs (Cabana & Rasmussen, 1996; Post, 2002).

It is well established that stable isotopes vary among habitats within (pelagic / benthic / littoral) and among lakes (France, 1995; Vander Zanden et al., 1999), and that this variation is key to understanding food web relationships. However, it is often assumed that spatial and temporal variation of isotope values within a single habitat type is relatively minor compared to food web fractionation processes. If within-habitat variation exists, it can confound the interpretation of stable isotopes and ultimately result in an erroneous assessment of food web structure and dynamics. Often this variation in stable isotopes within lakes is associated with

anthropogenic sources (Steffy & Kilman, 2004), such as sewage out flows (Savage, 2004) or near areas of increased urban populations, as seen on Lake Superior (Harvey & Kitchell, 2000). Stable isotopes have also been found to vary seasonally in particulate organic matter (Gu, 2009) and exhibit temporal variability in zooplankton due to changes in lipid content, growth rate (Matthews & Mazumder, 2005) and food source (Grey et al., 2001).

Recent research, however, has demonstrated that stable isotopes can also vary within a single lake habitat. For instance, Syvaranta et al., (2006) found temporal variation of $\delta^{15}\text{N}$ in pelagic particulate organic matter and zooplankton and spatial variation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values within both littoral and profundal communities of Lake Jyvasjari in Finland. Spatial variation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was also found in single species among canals in Xochilmilco, Mexico, a small, shallow, heterogeneous canal system with constant depth and sediment characteristics (Zambrano et al., 2010) and among sites of similar environmental characteristics in a variety of invertebrates and fish in Lake Kyoga, Africa (Mbabazi et al., 2010). There has been little effort, however, to quantify spatial and temporal variability of stable isotopes in important large lake systems, such as the Laurentian Great Lakes.

The western basin of Lake Erie represents one of the most productive and resilient food webs in the Great Lakes system and contributes approximately 30% of total Canadian freshwater commercial fish catches (Regier & Hartman, 1973; DFO, 2006). Using the western basin of Lake Erie as our test system, we examine the spatial and temporal variability of stable isotope across multiple lower trophic levels within the same habitat types, in the well mixed western basin of Lake Erie. We hypothesized that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ would vary spatially (within a single habitat zone), as a result of contrasting carbon/energy inputs in the lake. Because Lake Erie is temperate, we also hypothesized that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ would vary temporally throughout the growing season

(June - September), due to changes in nutrient inputs and changes in algal and zooplankton biodiversity. Finally, we examine the potential influence of spatial and temporal variability on food web structure assessment by examining TP estimates. Specifically we address the following questions: 1. Do spatial scale and temporal (four month period) variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ exist within lower trophic level species of the offshore habitat within the western basin of Lake Erie? 2. What are the implications of spatial and temporal variation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ on estimating TP and carbon sources of young-of-year (YOY) piscivorous fish (eg. White Perch (*Morone americana*) and Yellow Perch (*Perca flavescens*))?

Methods

Study Site

This study was implemented in the western basin of Lake Erie, a shallow (mean depth 7.5 m, maximum depth 10 m), flat basin that comprises the western third of Lake Erie. The basin is classified as mesotrophic (Kane et al., 2009), and is well mixed vertically with little or no significant summer stratification. Spatial complexity in the western basin of Lake Erie is a function of tributary and connecting channel hydraulic inputs. The basin has two major sources of nutrients, the Detroit and Maumee Rivers. Although the Detroit River's mean annual discharge is more than 35 times that of the Maumee ($5100 \text{ m}^3\text{s}^{-1}$ and $135 \text{ m}^3\text{s}^{-1}$), the Maumee River contributes ~ 35% of the total phosphorus load to the basin (Di Toro et al., 1987; Baker & Richards, 2002; Dolan & McGunagle, 2005) and provides warm nutrient rich waters which circulate in the southwest portion of the lake. The Detroit River provides a much larger flow of cooler nutrient limited waters and its plume extends well out into the basin (Reichert et al., 2010) (Fig. 1). Both the Maumee and Detroit River provide spatial and seasonal subsidies of nutrients, but also contribute to environmental heterogeneity with respect to water temperatures, plankton

communities, plankton and zooplankton production dynamics and fish assemblages (Barbiero et al., 2001; Reichert et al., 2010).

Sample Collection/ Analysis

Samples were collected from four locations across the western basin of Lake Erie (Fig. 2.1). Detroit River Plume and Middle Sister Island receive much of their water from Lake Huron while Maumee River Plume and Bass Islands are highly affected by spring melt water from the Maumee River basin, an area high in agriculture. At each location, seston samples were collected monthly from June-September 2009 using a 63 μm zooplankton net. In an effort to incorporate seston from the entire water column, vertical tows were conducted from one foot off bottom to the water surface. Bulk seston samples were frozen at -20°C in hexane rinsed polyethylene jars. Zebra mussels (*Dreissena polymorpha*) (June - September 2009) and YOY Yellow Perch (4.4 - 9.5 cm) and White Perch (3.2 – 8.4 cm) were collected by bottom trawls conducted as part of the Ontario Ministry of Natural Resources and Ohio Department of Natural Resources summer inter-agency trawls in July- September 2009. Both zebra mussels and YOY fish were frozen whole and brought back to lab in polyethylene sample bags. Zebra mussels were shucked to remove shells and were rinsed with distilled water. Samples were then pooled using 5-10 individuals of similar size to achieve sufficient sample for analysis and placed into cryo vials and frozen at -20°C . YOY fish dorsal muscle plugs were removed and placed into cryo vials and frozen at $\sim 20^{\circ}\text{C}$. For all species sampled, a minimum of three samples were collected per site, per sampling period (Table 2.1). Sample sizes for stable isotopes ranged from 3 to 9 replicates per species/site/month.

Prior to stable isotope analysis, samples were freeze dried for 48 hours and then ground with mortar and pestle in liquid nitrogen. Samples were weighed (800-1000 μg for seston, 400-

600 µg for zebra mussel and fish) into 0.5mg tin capsules and analyzed with a Delta V Advantage isotope ratio mass spectrometer (Thermo Electron Corporation, Bremen, Germany) and 4010 Elemental Combustion System (Costech Instruments, Valencia, CA, USA). At least 3 different lab and one NIST (8414) reference standards were used for quantification of stable isotope values and every tenth sample was run in triplicate to assess within run precision. Stable isotope values are conveyed in δ notation using the following equation:

$$\delta X = [R_{\text{sample}} / R_{\text{standard}} - 1] \times 1000$$

where X is ^{13}C or ^{15}N and R is the ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The standard reference material was Pee Dee Belemnite carbonate for C and atmospheric nitrogen N_2 for N. The analytical precision was based on the standard deviation of two standards (NIST 8218 bovine liver and internal fish standard; n=33 for each standard) and was 0.17‰ to 0.21‰ for $\delta^{15}\text{N}$ and 0.04‰ to 0.07‰ for $\delta^{13}\text{C}$. The analysis of NIST standards (sucrose and ammonia sulfate; n = 3 for each) during the analysis of samples generated values that were within 0.01‰ and 0.07‰ of certified values for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively.

Data Analysis

We used several statistical approaches to evaluate the effect of sampling site and sampling month on the isotopic values of western Lake Erie food web components and the estimated TP of White and Yellow Perch. To compare the isotopic composition of food web components between sampling sites we used repeated, linear mixed-effects models. Mixed-effects models are appropriate for these data structure encountered in this study, where samples collected across multiple months represent repeated measures of the same site (Raudenbush & Bryk, 2002). Therefore, to account for monthly variation both within and between sites our analytical design incorporated the random effect of monthly samples (treated as random

intercepts) nested within study site (treated as fixed effect). Further, to identify the proportional effect of monthly sampling within sites, we calculated the intraclass correlation coefficients (ICC), reflecting the proportion of variance attributable to each level of the model (i.e., sites and months within sites: see Raudenbush & Bryk, 2002).

To estimate the effects of sampling site and month on the TP of White and Yellow Perch we first estimated the TPs of the fish sampled using the following equation:

$$TP = [(\delta^{15}N_{\text{fish}} - \text{mean } \delta^{15}N_{\text{mussel}})/3.4] + 2$$

where the value 3.4 was used to denote an increase of one trophic level assuming zebra mussel occupy a TP of 2 (Post, 2002). We then developed a series of orthogonal contrasts to compare means of the estimated TPs of White and Yellow Perch between months within sites. We also used linear mixed models, controlling for the random effects of month, to see if the TP of White and Yellow Perch differed between sites. We then calculated TP of Yellow and White Perch from Detroit and Maumee using zebra mussels from different sites and months to demonstrate the relative importance of spatial and temporal variation in estimating TP in food webs of large lake ecosystems.

All statistical analyses were performed using the statistical package R (Version 2.11.1; R Development Core Team, 2010). Prior to analysis all stable isotopes data were tested for normality using probability plots and transformed where appropriate. For *post-hoc* multiple comparisons among fixed effects in models we used *Tukey* tests (Hothorn et al., 2008).

Results

Samples from the Maumee River Plume and Bass Island had higher $\delta^{13}C$ and $\delta^{15}N$ values than species from the Detroit River Plume and Middle Sister Island (Table 2.1). Our analysis revealed significant differences in both the $\delta^{13}C$ and $\delta^{15}N$ of seston ($\delta^{13}C$: $F_{3,61}=9.06$, $P<0.001$;

$\delta^{15}\text{N}$: $F_{3,61}=22.42$, $P<0.001$), zebra mussels ($\delta^{13}\text{C}$: $F_{3,47}=16.93$, $P<0.001$; $\delta^{15}\text{N}$: $F_{3,47}=45.53$, $P<0.001$), and Yellow ($\delta^{13}\text{C}$: $F_{3,54}=37.97$, $P<0.001$; $\delta^{15}\text{N}$: $F_{3,54}=24.17$, $P<0.001$) and White Perch ($\delta^{13}\text{C}$: $F_{3,45}=102.18$, $P<0.001$; $\delta^{15}\text{N}$: $F_{3,45}=60.81$, $P<0.001$) between sites (Table 2.2).

Temporal changes within site were found to contribute a significant proportion of the variation in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures for all species tested (Fig. 2.2) accounting for > 50% of variability in all species except seston (Table 2.2).

The TP of Yellow and White Perch differed significantly between sample sites and months within western Lake Erie ($F_{11,46}=23.68$, $P<0.001$, $F_{11,39}=28.92$, $P<0.001$) (Table 2.3). The TP of White and Yellow Perch from Maumee were significantly lower than the other sampling sites, which produced similar estimates. The TP of White and Yellow Perch were also found to differ between months within a site, with highest TP for each species across all sites found in August (Table 2.3). TP estimates for Yellow and White Perch also varied up to 0.7 when zebra mussels of non-corresponding sites and months were used to estimate TP (Table 2.3). In general, using zebra mussels from Maumee to estimate TP for Detroit fish resulted in an underestimation of TP, while using zebra mussels from Detroit to calculate TP of Maumee fish resulted in an overestimation of TP. Using zebra mussels from the same site but incorrect months also resulted in variable TP estimates in YOY White and Yellow Perch, however these differences were more prominent in fish from Maumee River Plume (Fig. 2.3).

Discussion

Our results reveal significant spatial and temporal variation in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of primary consumers and YOY fish in the offshore habitat of the western basin of Lake Erie. These results coincide with similar studies on other lake systems, which have found spatial variation in stable isotope values of organisms within the same habitat type (Syvaranta et al.,

2006; Mbabzi et al., 2010; Zambrano et al., 2010). For our model, month of collection explained the majority of the variation for all species except seston, indicating that temporal variability is a driving force of isotope variation within lower trophic levels of lake ecosystems. These findings are consistent with previous studies that have documented temporal variation in stable isotope values in particulate organic matter and zooplankton (Grey et al., 2001; Matthews & Mazumder, 2005; Syvaranta et al., 2006; Gu, 2009). Since trends in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values follow similar seasonal patterns across site, it suggests that spatial variation of stable isotopes in lower trophic level organisms is more a function of baseline effects rather than food web differences in Lake Erie. In essence, this variation represents the underlying biogeochemical differences among sites within a lake as suggested by Zambrano et al., (2010).

Spatial and temporal trends of stable isotopes were observed despite the fact that our samples were collected from sites of similar depth and habitat characteristics within the offshore habitat of the western basin of Lake Erie. The different characteristics of the two major rivers are very likely the source of the observed variation. The Maumee River catchment area is dominated by agriculture and urban run-off (Bolsenga & Herdendorf, 1993) and relative to more pelagic lake sources, these allochthonous sources are generally enriched in ^{13}C (Rounick et al., 1982) and ^{15}N (Diebel & Vander Zanden, 2009). On the other hand, the Detroit River is predominantly water from the Lake Huron and would be expected to have lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values representative of autochthonous lake sources (see Hebert et al., 1999; Fox et al., 2002; Paterson et al., 2006). Stable isotope values in all samples from June and July followed expected patterns based on the river of influence, but in August and September, stable isotope values were relatively similar across sampling sites. Overall, stable isotope values from August and September were more consistent with values observed in June and July at Detroit River plume,

suggesting that the influence of the early spring run-off of the Maumee River on stable isotope values in lower trophic level species had declined.

Month was found to be a more important variable than location in contributing to variation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in zebra mussels and YOY Yellow and White Perch across the Western Basin of Lake Erie. These temporal contributions reflect the fact that Lake Erie is located in a temperate climate area, and as a result, seasonal runoff, primary production, algal content and food web dynamics vary through the open-water season, all of which have been shown to influence stable isotope values. Monthly variability was evident in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in all species and sites. Isotope values at Detroit/Middle Sister and Maumee/Bass were closely related to one another as would be predicted by water current patterns within the lake (Kovacik, 1972; Bolsenga & Herdendorf, 1993). In general, species became more enriched in both ^{13}C and ^{15}N from early summer to fall, likely as a result of the loss of terrestrial runoff sources which are documented to spike in spring (Richards et al., 2008). While isotopic values for all species varied among sites, these values exhibited similar trends in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from spring through fall, confirming that these isotopic differences are linked to baseline effects rather than food web differences (Zambrano et al., 2010).

Differences among species were more pronounced in $\delta^{15}\text{N}$ rather than $\delta^{13}\text{C}$ values. Seston had a slightly higher $\delta^{15}\text{N}$ signature than zebra mussels, which could be a result of sediment disturbance events, potentially increasing the organic/ inorganic content of seston. Increases in $\delta^{15}\text{N}$ in the seston could reflect increases in zooplankton population later in the season (Fahnenstiel et al., 1998); seston samples were not sorted. Zebra mussels $\delta^{15}\text{N}$ values spiked in June and September, while decreasing during July and August. Increases in YOY fish $\delta^{15}\text{N}$ are most likely a function of fish growth and resulting diet changes similar to YOY smallmouth bass

(*Micropterus dolomieu*) whose $\delta^{15}\text{N}$ were correlated with growth (Vander Zanden & Rasmussen, 1998), but also partially due to an increase in the value of $\delta^{15}\text{N}$ in the system. Young of year Yellow and White Perch typically hatch late April through June in the western basin (Ludsin & Devries, 1997), with White Perch hatching slightly before Yellow Perch (T. Johnson, *personal communication*), explaining the slightly higher $\delta^{15}\text{N}$ of White Perch. During this time Yellow Perch typically undergo a diet shift from pelagic to demersal when they reach about 20-25 mm in length (Wu & Culver, 1992), while White Perch remain in shallow waters. White Perch have a more terminal mouth, advantageous for feeding up in the water column on plankton. Yellow Perch on the other hand, have a sub-terminal mouth, allowing for easier benthic feeding (Parrish & Margraf, 1990). While YOY of both species have been found to feed relatively similarly in laboratory studies (Parrish & Margraf, 1990) the $\delta^{13}\text{C}$ observed in this study suggest that feeding strategies of the two species may be different.

Estimates of TP based on the $\delta^{15}\text{N}$ of fish relative to a sessile baseline species have become increasingly popular in food web studies (Vander Zanden et al., 1997). Evidence of spatial zones and monthly variability of $\delta^{15}\text{N}$ in this study suggests a potential impact on the accuracy of TP estimations. Monthly differences in TP could be a result of changes in feeding behavior with growth of YOY fish as found in YOY black bass (Vander Zanden & Rasmussen, 1998) or differences in baseline $\delta^{15}\text{N}$ values in zebra mussels due to variation in nitrogen flow across the basin. We quantified large variations in the TP estimates for both Yellow and White Perch when using a baseline collected from an incorrect site or month in the calculation. These differences were most pronounced when mussels from incorrect sites were used for TP calculation of the fish. Using zebra mussels from incorrect months led to relatively smaller variations, suggesting that baseline differences among sites are an important factor to consider

when estimating TP using $\delta^{15}\text{N}$ values of species relative to $\delta^{15}\text{N}$ of sessile baseline organism. This also highlights the importance of consistency in sampling design, ensuring that sessile baseline organisms used in TP calculations are sampled from the same location/timeframe as the organisms being estimated for.

In general, many studies that have used stable isotopes to examine food webs have been coarse in their descriptions of food web structure and links. As the use of stable isotopes becomes more quantitative (e.g., Layman et al., 2007; Hoffman et al., 2010) it becomes necessary that we understand and incorporate this variation in stable isotopes values into studies on food web structure and function. Within habitat variation of isotopes in large lakes could be problematic when trying to distinguish carbon and nitrogen sources in systems with multiple nutrient inputs. The calculation of TP for organisms acquiring nitrogen from multiple sources requires the use of base $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from each nutrient input (Post, 2002). However, if significant temporal variation exists within single sites, even in primary consumers, which are thought to absorb temporal variance of isotopic values (Vander Zanden and Rasmussen, 1999), then uncertainties could arise in the determination of true isotopic values of each contributing nutrient source. The significance of incorrect TP assignment was demonstrated recently; where Branch et al., (2010) discovered that a 0.5 change in TP of anchoveta resulted in an erroneous report of steep declines in global fisheries landings since the 1970s, as described in the benchmark work of Pauly et al. (1998). While this degree of error in TP estimates would typically be considered minor or inconsequential in many food web studies, it altered the global catch mean trophic level trend reported by Pauley et al. (1998). These findings highlight the sensitivity of fisheries management techniques to variation in TP estimates. While, primary consumers do provide appropriate baselines for qualitative use of stable isotopes, we have

demonstrated that they are susceptible to substantial spatial and temporal variation, which could hinder the evolution of stable isotopes as a quantitative tool in food web studies.

Acknowledgments

Sandra Ellis, Anna Hussey, Eric Primeau, Mary-Lynn Mailloux, Carly Ziter and Kristen Diemer are thanked for their valuable assistance in the laboratory. Craig MacDonald and the staff at the Ministry of Natural Resources Lake Erie Management Unit and Eric Weimer and the staff at the Ohio Department of Natural Resources Sandusky Fish Research Unit are thanked for their help in sample collection. James Vaillant is thanked for his help making the map. This work was funded by Canada Research Chair funds awarded to A.T. Fisk and G.D. Haffner and graduate assistantships awarded to M. Guzzo from the University of Windsor.

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Table 2.1. Spatial and temporal variability of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for seston, zebra mussels, Yellow Perch and White Perch from the Western Basin of Lake Erie. Values are means \pm 1 SE.

Species	Month	n	Maumee River Plume		n	Bass Island		n	Detroit River Plume		n	Middle Sister Island	
			$\delta^{13}\text{C} \text{ ‰}$	$\delta^{15}\text{N} \text{ ‰}$		$\delta^{13}\text{C} \text{ ‰}$	$\delta^{15}\text{N} \text{ ‰}$		$\delta^{13}\text{C} \text{ ‰}$	$\delta^{15}\text{N} \text{ ‰}$		$\delta^{13}\text{C} \text{ ‰}$	$\delta^{15}\text{N} \text{ ‰}$
Seston	June	3	-28.0 ± 0.38	8.59 ± 0.06	5	-27.1 ± 0.06	6.72 ± 0.06	3	-24.6 ± 0.04	7.00 ± 0.02	3	-25.4 ± 0.14	5.77 ± 0.30
	July	7	-25.4 ± 0.03	6.22 ± 0.09	5	-26.7 ± 0.03	8.78 ± 0.09	3	-24.1 ± 0.09	6.10 ± 0.34	3	-25.0 ± 0.04	6.66 ± 0.08
	August	7	-23.7 ± 0.06	7.96 ± 0.06	5	-25.8 ± 0.05	10.2 ± 0.15	3	-25.0 ± 0.10	6.75 ± 0.11	3	-22.7 ± 0.03	3.63 ± 0.45
	September	3	-24.6 ± 0.04	10.0 ± 0.11	3	-24.0 ± 0.19	9.72 ± 0.01	5	-25.9 ± 0.04	5.68 ± 0.07	5	-24.6 ± 0.09	6.08 ± 0.13
Zebra mussel	June	3	-26.6 ± 0.04	8.07 ± 0.06	5	-25.3 ± 0.18	10.1 ± 0.08	3	-23.3 ± 0.16	6.82 ± 0.19	3	-25.1 ± 0.17	6.87 ± 0.18
	July	3	-25.6 ± 0.07	7.31 ± 0.03	3	-26.2 ± 0.26	7.32 ± 0.08	3	-23.3 ± 0.14	6.46 ± 0.05	5	-24.9 ± 0.20	6.09 ± 0.09
	August	3	-26.3 ± 0.74	7.38 ± 0.05	5	-25.4 ± 0.50	7.23 ± 0.15	3	-22.4 ± 0.09	6.43 ± 0.11	3	-22.8 ± 0.07	5.99 ± 0.06
	September	3	-22.8 ± 0.10	9.12 ± 0.15	3	-22.5 ± 0.15	9.30 ± 0.27	3	-22.8 ± 0.22	6.90 ± 0.16	3	-21.7 ± 0.83	6.71 ± 0.21
Yellow Perch	July	3	-24.8 ± 0.06	11.3 ± 0.05	5	-24.6 ± 0.07	11.4 ± 0.10	3	-22.0 ± 0.04	11.1 ± 0.05	3	-22.9 ± 0.04	11.0 ± 0.07
	August	5	-23.3 ± 0.18	11.5 ± 0.13	4	-23.0 ± 0.17	13.1 ± 0.15	7	-21.8 ± 0.17	11.6 ± 0.16	3	-22.1 ± 0.06	11.4 ± 0.09
	September	7	-21.4 ± 0.16	12.2 ± 0.20	6	-22.4 ± 0.05	13.2 ± 0.07	9	-20.8 ± 0.17	12.1 ± 0.21	7	-21.0 ± 0.25	11.7 ± 0.18
White Perch	July	3	-25.1 ± 0.33	11.8 ± 0.22	7	-24.7 ± 0.04	12.2 ± 0.13	3	-20.7 ± 0.08	10.8 ± 0.06	3	-21.2 ± 0.15	10.9 ± 0.02
	August	5	-22.3 ± 0.18	12.0 ± 0.11	5	-23.9 ± 0.11	13.8 ± 0.27	4	-20.4 ± 0.07	11.3 ± 0.13	3	-20.7 ± 0.10	11.3 ± 0.03
	September	5	-21.6 ± 0.09	12.8 ± 0.17	5	-23.1 ± 0.10	14.4 ± 0.10	4	-20.2 ± 0.12	12.9 ± 0.16	4	-20.8 ± 0.18	12.3 ± 0.08

^a n refers to the number of samples, samples were pools of multiple individuals for seston and zebra mussel only.

Table 2.2. Tukey post-hoc comparisons between sites for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of all species from the Western Basin of Lake Erie.

Species	Isotope		Site differences						Variability attributed by month (%)
			DET-BS	ME-BS	MSI-BS	ME-DET	MSI-DET	MSI-ME	
Seston	$\delta^{13}\text{C}$	Estimate	1.01	0.89	1.6	-0.12	0.62	0.74	47
		P	0.0089*	0.012*	<0.001*	0.98	0.28	0.10	
	$\delta^{15}\text{N}$	Estimate	-2.4	-0.86	-3.08	1.6	-0.67	-2.2	27
		P	<0.001*	0.11	<0.001*	0.0012*	0.45	<0.001*	
Zebra mussel	$\delta^{13}\text{C}$	Estimate	1.9	-0.42	1.2	-2.4	-0.76	1.6	57
		P	<0.001*	0.63	0.0033*	<0.001*	0.17	<0.001*	
	$\delta^{15}\text{N}$	Estimate	-1.9	-0.57	-2.1	1.3	-0.205	-1.5	75
		P	<0.001*	0.42	<0.001*	<0.001*	0.79	<0.001*	
Yellow Perch	$\delta^{13}\text{C}$	Estimate	1.7	0.36	1.3	-1.3	-0.37	0.95	68
		P	<0.001*	0.21	<0.001*	<0.001*	0.21	<0.001*	
	$\delta^{15}\text{N}$	Estimate	-1.03	-0.94	-1.3	0.089	-0.26	-0.35	58
		P	<0.001*	<0.001*	<0.001*	0.94	0.37	0.16	
White Perch	$\delta^{13}\text{C}$	Estimate	3.4	1.1	2.9	-2.3	-0.50	1.8	58
		P	<0.001*	<0.001*	<0.001*	<0.001*	0.19	<0.001*	
	$\delta^{15}\text{N}$	Estimate	-1.7	-1.3	-1.9	0.42	-0.18	-0.61	68
		P	<0.001*	<0.001*	<0.001*	0.058	0.74	0.0027*	

* Indicates comparison is significant at $\alpha=0.05$.

^a Estimate denotes the mean difference between sites, while P reflects statistical significance with $\alpha < 0.05$ considered statistically significant. Percent variability by month reflects the percent of variation attributed by month in the model for the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of each species. ME=Maumee River Plume, BS= Bass Islands, DET= Detroit River Plume, MSI= Middle Sister Island.

Table 2.3. Mean TP estimates from bootstrapping with orthogonal contrasts of months within site and Tukey post hoc comparisons between sites from the Western Basin of Lake Erie.

Species	Mean TP estimates				Monthly differences within site		Site differences		
	Site	July	Aug	Sept	Statistical significance of orthogonal contrasts (P)		Comparison	Estimate	P
Yellow Perch							BS-ME	0.083	<0.001*
	ME	3.2	3.2	2.9	0.10	<0.001*	DET-ME	0.12	<0.001*
	BS	3.2	3.7	3.2	<0.001*	<0.001*	MSI-ME	0.13	<0.001*
	DET	3.4	3.5	3.6	0.03*	0.11	DET-BS	0.041	0.079
	MSI	3.4	3.6	3.5	0.29	0.40	MSI-BS	0.048	0.059
							MSI-DET	0.006	0.98
White Perch							BS-ME	0.11	<0.001*
	ME	3.3	3.4	3.1	0.08	<0.001*	DET-ME	0.083	<0.001*
	BS	3.4	3.9	3.5	<0.001*	<0.001*	MSI-ME	0.098	<0.001*
	DET	3.3	3.4	3.8	<0.001*	<0.001*	DET-BS	-0.030	0.39
	MSI	3.4	3.6	3.6	0.75	<0.001*	MSI-BS	-0.015	0.86
							MSI-DET	0.014	0.90

* Indicates comparison is significant at $\alpha=0.05$.

^a Estimate denotes the mean differences between sites; P reflects statistical significance. ME=Maumee River Plume, BS= Bass Islands, DET= Detroit River Plume, MSI= Middle Sister Island.

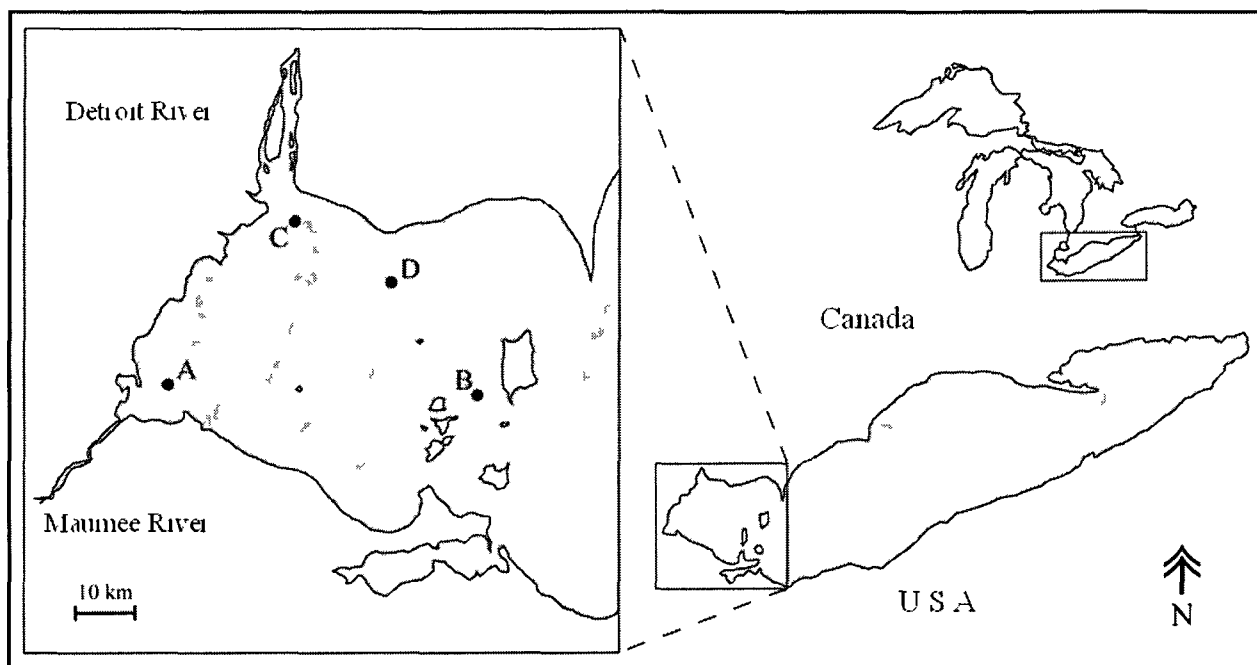


Figure 2.1 Location of sampling sites in the western basin of Lake Erie, sampled during June-September 2009. Letters A-D represents fixed sampling site. A= Maumee River Plume, B= Bass Islands, C= Detroit River Plume, D= Middle Sister Island.

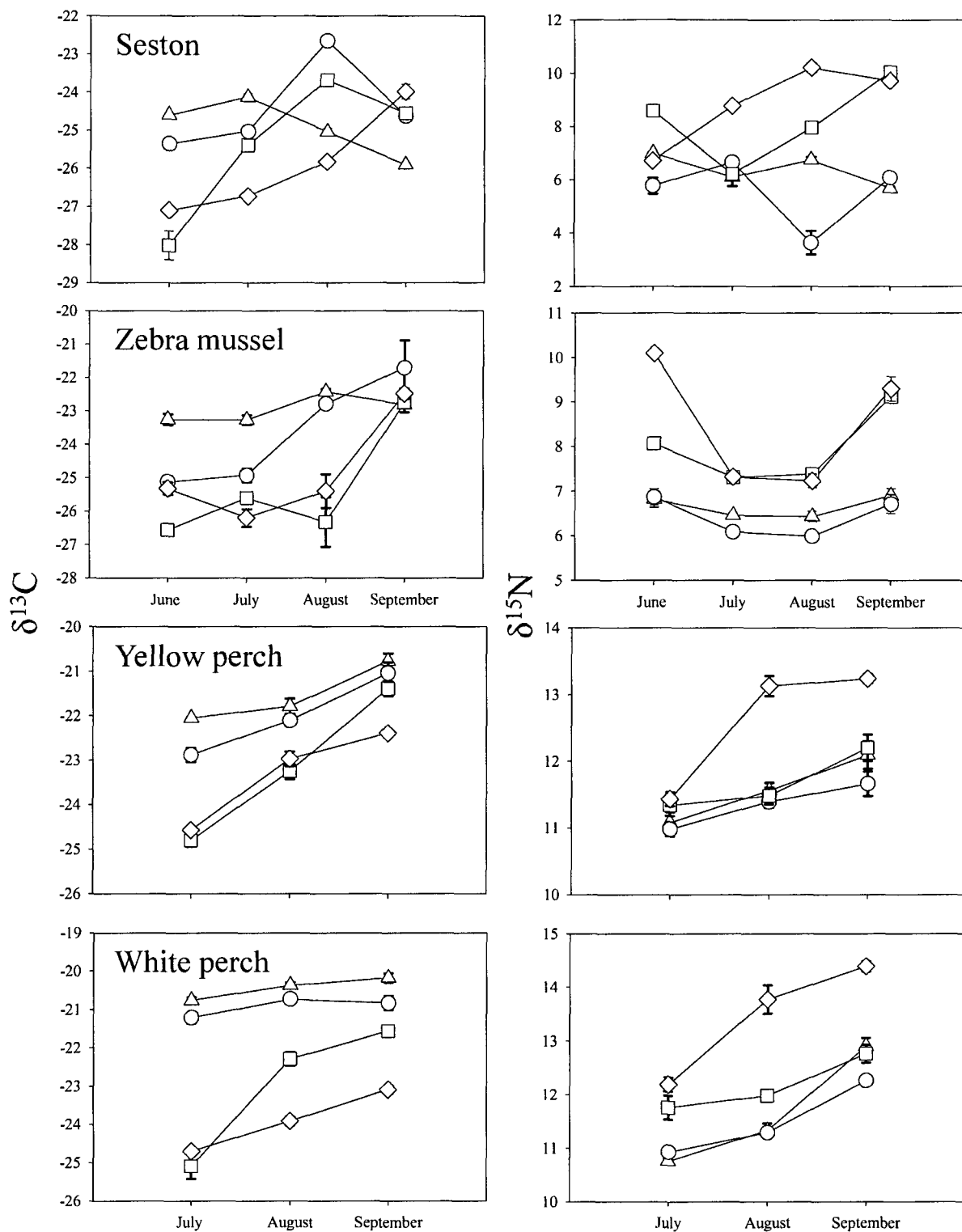


Figure 2.2 Temporal patterns of mean stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) values ($\pm 1\text{SE}$) in the western basin of Lake Erie during 2009. In each graph squares= Maumee River Plume, diamonds= Bass Islands, circles= Middle Sister Island, triangles= Detroit River Plume.

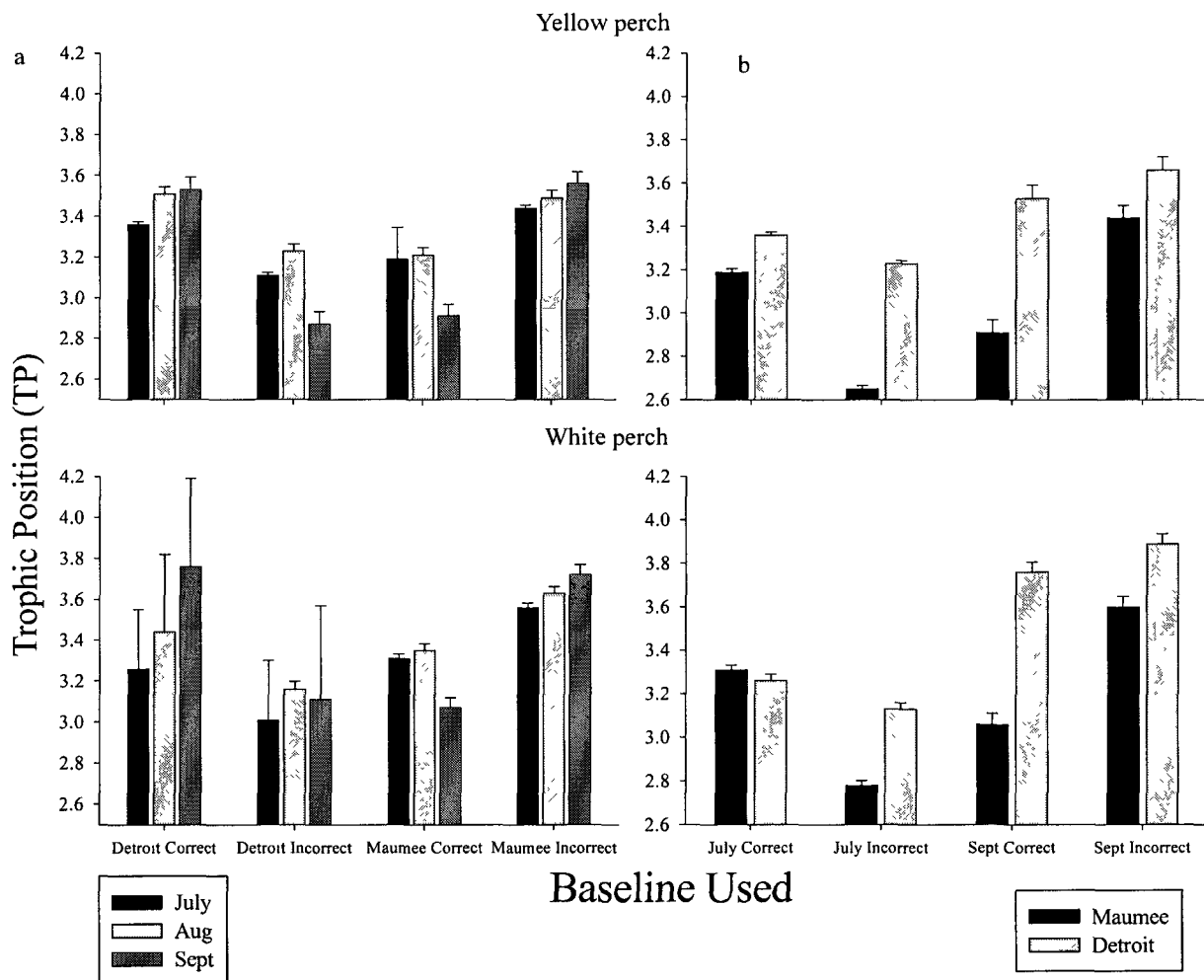


Figure 2.3 Trophic position estimates for Yellow and White Perch using zebra mussel baselines collected from the same site/month as fish (Correct) and using zebra mussels from a different month/site (Incorrect). For graph 'a' YOY Yellow and White Perch collected from Maumee River Plume and Detroit River Plume are calculated using zebra mussels from the corresponding location and using zebra mussels from non-corresponding locations (i.e. Detroit fish using Maumee mussels), respectively. For graph 'b' YOY Yellow and White Perch collected from July and September are calculated using zebra mussels from the corresponding month and using zebra mussels from non-corresponding months (i.e. July fish using September mussels).

CHAPTER 3

RESOURCE UTILIZATION AND NICHE OVERLAP OF A NATIVE AND INVASIVE FISH SPECIES IN THE WESTERN BASIN OF LAKE ERIE

Introduction

Non-native, or invasive, species are present in most regions of the planet, and a number of these invaders threaten biodiversity, ecosystem function and natural resources (Vitousek et al., 1997; Mack et al., 2000). The majority of invasive species introductions are attributed to human activities and international trade (Mack & Lonsdale, 2001; Levine & D'Antonio, 2003) and as a result invasions are occurring over unprecedented spatial and temporal scales, particularly in large aquatic ecosystems (Cohen & Carlton, 1998; Ruiz et al., 2000; Ricciardi, 2006). Many successful invasive species are classified as trophic generalists (Marvier, 2004), characterized by their wide ecological tolerance, allowing them to be highly successful in new habitats (Sax and Brown 2000; Polo-Cavia et al., 2008). Once established, invasive species have the potential to compete with native species, often resulting in declines of native species populations and diversity (Sakai et al., 2001; Michelan et al., 2010), ultimately influencing population dynamics and community structure in diverse ecosystems (Baxter et al. 2004). Many studies examining interactions among aquatic native and invasive species have focused on newly introduced species or cases where invasions have resulted in significant declines of native species (e.g. Benoit et al., 2002; Wilson et al., 2004). However, fewer studies have focused on co-existing invasive and native fish species in a previously invaded large lake.

The Laurentian Great Lakes have experienced cascading ecological effects from over 180 invasive species (Holeck et al., 2004) and as a result many scientists and lake managers recognize the importance in understanding the interactions among native and invasive fish species (Britton et al., 2010). The western basin of Lake Erie has not exhibited the degree of trophic change evident in the food webs of Lakes Huron, Ontario, Michigan and Superior as a result of invasive species (e.g. Eshenroder 1995; Hansen et al., 1995; Holey et al., 1995; Mills et

al., 2003). One important invader is the White Perch (*Morone Americana*), an east coast estuarine fish, first collected in Lake Erie in 1953, which proliferated in the mid 1970s (Larsen 1954; Parrish & Margraf, 1990). Commercial catches of White Perch in the western basin increased greatly in the 1980s and early studies based on gut content analysis found White Perch feeding strategies to be very similar to those of Yellow Perch and suggested the two species could be in direct competition for resources (Schaeffer & Margraf 1986 a, b; Parrish & Margraf 1990; 1991; 1994). Since these early studies there have been substantial changes to the benthic community of the western basin of Lake Erie. The exotic zebra mussel (*Dreissena polymorpha*) has colonized and spread throughout the lake and now comprises 80-90% of benthic biomass (Tyson & Knight, 2001). Large benthic invertebrates such as *Hexagenia*, caddisfly nymphs (Trichoptera) and amphipods have recolonized the western basin and have been linked to increased growth and recruitment of Yellow Perch (*Perca flavescens*) (Tyson & Knight, 2001), a species that has historically been an abundant and highly valuable fish species sought after both commercially and recreationally in Lake Erie. White Perch are also harvested in the basin, but to a lesser degree than Yellow Perch, as they have much lower commercial value (Kinnunen, 2003). Recently there have been concerns about the Yellow Perch population in the basin and as a result fishing quotas have been cut (Yellow Perch Task Group, 2010). While relative abundance of Yellow and White Perch seems to have stabilized (Fig. 3.1), current Yellow Perch biomass and populations in the western basin of Lake Erie still remain lower than historical values (Yellow Perch Task Group, 2010), and questions remain as to whether similar feeding habits and significant biomass of White Perch are limiting populations of the more commercially favored Yellow Perch within the basin.

Despite the economic and ecological importance of the Yellow Perch and the potential niche overlap with the non-native White Perch, there is a general lack of information on the feeding ecology of Yellow and White Perch in the western basin of Lake Erie. This basin experiences large spatial variability in nutrient inputs, which can influence trophic relationships (Armitage and Fourqurean, 2009; Guzzo et al. 2010). Both species have been shown to experience ontogenetic shifts in diet early in life (Parrish and Margraf 1990; 1991), so the potential niche overlap of these species could be complex and significant to perch populations and general ecosystem structure. To address these data gaps we analyzed stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in the muscle tissue of adult Yellow and White Perch, at four locations in the western basin of Lake Erie. Samples of zebra mussels were also collected at all sites to baseline stable isotopes in fish (Post et al 2002) and allow spatial variability in stable isotopes to be accounted for (Guzzo et al. 2010). Stable isotopes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ have been widely used to describe food web structure for aquatic ecosystems (Peterson & Fry, 1987) and provide a means to examine the trophic niches of individual species (Zambrano et al., 2010). Our objectives were two-fold: 1) to examine the carbon sources and trophic position of adult Yellow and White Perch across the western basin of Lake Erie through body size; 2) to examine niche overlap between a commercially-important native and a non-native fish species.

Methods

Study Site

Samples were collected in the western basin of Lake Erie (Fig. 3.2), a shallow (average depth 7.5 m, maximum depth 10 m), flat basin making up the western third of Lake Erie, part of the Laurentian Great Lakes system. The basin is classified as mesotrophic (Kane et al. 2009), and is vertically mixed with limited summer stratification. The western basin of Lake Erie is spatially

complex as a result of tributary and connecting channel hydraulic inputs. The basin has two major water inputs, the Detroit and Maumee Rivers. Although the Detroit River's mean annual discharge is more than 35 times that of the Maumee ($5100 \text{ m}^3\text{s}^{-1}$ and $135 \text{ m}^3\text{s}^{-1}$), the Maumee River contributes ~ 35% of the total phosphorous load to the basin (Di Toro et al. 1987; Baker and Richards 2002; Dolan and McGunagle 2005) and provides warm nutrient rich waters which circulate in the southwest portion of the lake. The Detroit River provides a much larger flow of relatively cooler, nutrient limited waters and its plume extends well out into the basin (Reichert et al. 2010) (Fig. 3.2). Differences in the contributing water from the Maumee and Detroit River provide spatial and seasonal subsidies of nutrients and energy, but also contribute to environmental heterogeneity with respect to water temperatures, plankton communities, plankton and zooplankton production dynamics and fish assemblages (Barbiero et al. 2001a,b; Reichert et al., 2010). These physical and biophysical attributes provide important spawning, nursery habitats and forage bases for several native predatory fish species including these Yellow Perch (Zhao et al., 2009; Reichert et al., 2010).

Sample Collection and Analysis

Fish and zebra mussels were collected using bottom trawls and gill nets employed at four sites in the western basin of Lake Erie (Fig. 3.2) from April to September of 2009 as part of the Ontario Ministry of Natural Resources and Ohio Department of Natural Resources summer inter-agency trawls (Tyson et al., 2006). Detroit River and Middle Sister Island sites are both located in what we refer to as the Detroit plume, while Maumee River and Bass Island sites are in the Maumee plume. These plumes were established based on lake water current patterns and baseline isotopic values of lower food web species (Kovacik, 1972; Bolsenga and Herdendorf, 1993; Guzzo et al., 2010). Zebra mussels were collected to provide information regarding

baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at each sampling location. Both zebra mussels and fish were frozen whole and brought back to lab. In the lab, zebra mussels were shucked to remove shells, rinsed with distilled water, and then pooled into single samples of 5-10 individuals of similar size to achieve sufficient sample for analysis and frozen at -20°C . Fish dorsal muscle plugs were removed and frozen at $\sim 20^{\circ}\text{C}$, and 12-32 individuals of a species were collected per site (Table 3.1).

A total of 280 samples were freeze-dried and analyzed for stable isotopes using a Delta V Advantage isotope ratio mass spectrometer (Thermo Electron Corporation, Bremen, Germany) and 4010 Elemental Combustion System (Costech Instruments, Valencia, CA, USA). Stable isotope values are conveyed in δ notation where $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The standard reference material was Pee Dee Belemnite carbonate for CO_2 and atmospheric nitrogen for N_2 . At least 3 different lab and one NIST (8414) reference standards were used for quantification of stable isotope values and every tenth sample was run in triplicate to assess within run precision. The analytical precision based on the standard deviation of an internal lab (fish muscle) and NIST standard 8414 (bovine liver) for $\delta^{15}\text{N}$ ($n = 55/\text{standard}$) were 0.16‰ to 0.20‰, respectively, and for $\delta^{13}\text{C}$ were 0.05‰ to 0.07‰, respectively, during the analysis of these samples. The analysis of NIST standards (sucrose and ammonia sulphate; $n = 3$ for each) during the analysis of samples generated values that were within 0.01‰ and 0.07‰ of certified values for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively.

Data Analysis

Prior to analysis all length and stable isotope data were determined to be normally distributed based on probability plots for each species and location. Stable isotope data for sampling months were combined over the entire summer because stable isotope turnover times for fish muscle of this size would be on the order of months (Perga and Gerdeaux, 2005). Sites

were kept separate to provide insight into the feeding and overlap of species across sites of varying physical and biological characteristics and because of known spatial variability of isotopes in this system (Guzzo et al. 2010). However, to provide a basin-wide comparison of the species, statistical analysis was also carried out on data for all sites combined, referred to as *basin-wide*.

Linear regressions were used to examine relationships between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with fish total length for each sampling location and species (Body length=species+site+speciesxsite). We used t-tests to determine if mean fish length differed between fish species and MANOVA to test for the effects of species, site and species x site. We also used ANOVA with *Tukey post-hoc* to determine difference in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among species at all sampling locations.

Trophic positions were estimated using the equation:

$$\text{trophic position} = [(\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{zebra mussel}})/3.4] + 2 \quad (1),$$

where, 3.4 denotes the increase of $\delta^{15}\text{N}$ for one trophic level (often called a diet-tissue discrimination factor) and assuming zebra mussel occupy a trophic position of two (Post 2002). Trophic positions were calculated for each species at each site using $\delta^{15}\text{N}$ of zebra mussel collected from that site, to eliminate the potential bias caused by spatial variability in $\delta^{15}\text{N}$ values between sites within this lentic system (Guzzo et al. 2010).

Trophic niche variables and niche space were calculated using $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-pots according to Layman et al. (2007), allowing for comparison of niche partitioning across species and sites. We adapted this technique to evaluate the trophic niche of individual species, rather than a community as originally described (Zambrano et al. 2010). Values used to compare the ‘niche width’ were based on nitrogen range (NR), carbon range (CR) and total niche area (TA) of adult Yellow Perch and White Perch. NR is defined as the difference between the highest and

lowest $\delta^{15}\text{N}$ value of each species providing insight into feeding behavior and nitrogen sources of specific age/species. CR is defined as the highest and lowest $\delta^{13}\text{C}$ of each species, describing the breadth of food sources being consumed by that specific age/species. The total niche area (TA) was determined for a species and calculated from the convex hull area in the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plot (Layman et al. 2007). We grouped fish isotope values across all sampling months to compare the niche widths among species across the system and at each sampling location. We then calculated the site specific CR and NR of zebra mussels to provide a “resource availability baseline” so that available range of carbon and nitrogen resources each sampling site could be used to help understand potential differences in NR, CR and TA of each species across sites.

All t-tests and linear regressions were performed using the statistical program SYSTAT (Version 11; Systat Software Inc. Chicago, IL, USA). MANOVA, ANOVA and convex hull areas of $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plot were performed using the statistical package R (Version 2.11.1; R Development Core Team, 2010). All analyses were considered statistically significant at $P < 0.05$.

Results

There were no basin-wide or site specific differences in length between Yellow Perch and White Perch ($t = -1.23$, $df = 215$, $P = 0.217$), except that White Perch were significantly larger than Yellow Perch at Detroit River (Table 3.1).

For Yellow Perch, there was a very weak positive relationship between $\delta^{15}\text{N}$ and fish length for basin-wide ($F_{1, 105} = 4.53$, $P = 0.04$, $R^2 = 0.04$) and at Maumee River plume sites (i.e., Maumee River and Bass Islands), however much stronger relationships were found at sites within the Detroit River plume (i.e., Detroit River and Middle Sister Island) (Fig. 3.3). There was no relationship between fish length and $\delta^{13}\text{C}$ values for Yellow Perch at any site. White Perch, $\delta^{15}\text{N}$ values were positively related to fish length both basin-wide ($F_{1, 108} = 22.36$, $P = < 0.001$,

$R^2=0.17$) and at all sampling locations except Bass Island (Fig. 3.3). There was no relationship between $\delta^{13}\text{C}$ values and fish length for White Perch.

MANOVA using both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ revealed significant effects of the variables species and sampling site, but no significant interaction (Table 3.2). These effects were also significant considering $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ alone using ANOVA (Table 3.2). The two fish species tested (Yellow Perch and White Perch) were found to be significantly different in their isotopic values, with Yellow Perch being more enriched in $\delta^{13}\text{C}$ and depleted in $\delta^{15}\text{N}$ than White Perch across all sampling locations as indicated by *Tukey post-hoc* tests (Fig. 3.4).

Individual sampling sites exhibited significant isotopic differences (Table 3.3; Fig. 3.5). Detroit and Middle Sister Island had enriched $\delta^{13}\text{C}$ values compared to Maumee and Bass Island, however, differences among sites were driven by significantly more enriched $\delta^{13}\text{C}$ at Detroit than all other sites. The $\delta^{15}\text{N}$ of fish were relatively similar among sampling locations, where Bass Island exhibited highest $\delta^{15}\text{N}$ values and Middle Sister Island exhibited lowest $\delta^{15}\text{N}$ values (Fig. 3.5)

Stable isotope bi-plots comparing trophic niche areas and food web metrics indicate high overlap in the niche space of Yellow and White Perch (Fig. 3.6). The largest TAs, NRs and CRs were associated with the Maumee River sites for both species, while White Perch had higher TA values across all sampling sites (Table 3.4).

Discussion

Carbon and nitrogen stable isotopes values in muscle revealed that populations of native Yellow Perch and non-native White Perch are utilizing different carbon sources and feeding at different trophic levels across the western basin of Lake Erie. White Perch had larger niche widths and fed at a higher trophic position and more pelagic forage base than the Yellow Perch.

Although the species were different in their mean isotopic values, overlap of niche areas indicate that some individuals of these species utilize similar forage bases. Both species showed increases in trophic position with size based on $\delta^{15}\text{N}$, although these relationships were not significant at all locations. The relative feeding ecology of these two species varied with sampling location, suggesting that different nutrient and temperature characteristics may influence the trophic relationship between these species. These results provide evidence that changes in prey abundance or distribution could result in Yellow and White Perch competing for resources in the western basin of Lake Erie.

Yellow Perch and White Perch have both been described as opportunistic, omnivorous feeders (Parrish & Margraf, 1990; Campbell et al., 2009), however they were found to differ in their primary carbon sources. Mean basin-wide $\delta^{13}\text{C}$ values of Yellow (-21.9‰) and White Perch (-22.6‰) were enriched compared to $\delta^{13}\text{C}$ values of zebra mussel (-24.3‰), which filter pelagic food sources, and those recently reported for zooplankton (-23.6‰; Garton et al., 2005) indicating both species included ^{13}C enriched benthos in their diet as indicated by previous studies in the western basin (Parrish & Margraf, 1990; Parrish & Margraf, 1994 ; Legler, *unpublished*). The $\delta^{13}\text{C}$ values indicated that Yellow Perch rely on a more benthic food source than White Perch in the western basin of Lake Erie, which is consistent with other stable isotope and diet studies of these species in both Lake Erie (Parrish & Margraf, 1994; Legler, *unpublished*; Campbell et al., 2009) and other systems (Prout et al., 1990; White & Facey, 2009). Decreased foraging on zooplankton and increased consumption of mayflies, zebra mussels and soft rayed fish by Yellow Perch relative to White Perch (Legler, *unpublished*), in addition to physical constraints (gape position) on benthic foraging by White Perch (Parrish and Margraf, 1990) provide explanation for Yellow Perch's enriched $\delta^{13}\text{C}$ values relative to White Perch.

Differences in diet, inferred by stable isotopes and comparison with the sessile filter feeding zebra mussels, among Maumee plume and Detroit plume fish were presumably the result of differences in prey availability and abundance and/or environmental characteristics of the sampling locations. Yellow and White Perch were more enriched in ^{13}C at Detroit plume sites relative to Maumee plume sites indicative of a more benthic source of carbon at Detroit. This is consistent with a recent work that found both species to consume increased amounts of zooplankton in the Maumee plume and increased benthos and fish at Detroit plume (Legler, *unpublished*). These differences among sites could also be a result of differences in the source of river water between Detroit and Maumee Rivers. Maumee River represents a terrestrial source of carbon to the system, which are typically more depleted in ^{13}C ($\sim -27\text{‰}$ for C^3 photosynthetic plants; Peterson & Fry, 1987), while Detroit river receives water from Lake Huron which is more enriched in ^{13}C (Guzzo et al., 2010). These isotopic differences in source water among sites are typically reflected in the base of the food web and transferred up the food web to consumers resulting in variations in stable isotope values (Peterson & Fry, 1987).

White Perch had enriched $\delta^{15}\text{N}$ values, and higher trophic positions using zebra mussels as a baseline, than Yellow Perch across all sampling locations. For the size of fish collected in this study, White Perch in western Lake Erie have been found have a greater size at age values than Yellow Perch (OMNR, *unpublished data*), this increased size has been shown to be correlated to higher $\delta^{15}\text{N}$ values (Layman et al., 2005) and could provide explanation for White Perch occupying higher trophic positions than Yellow Perch. Another possible explanation for enriched $\delta^{15}\text{N}$ of White Perch could be due to increased consumption of zooplankton relative to Yellow Perch. A study by Vander Zanden et al., (1997) found that Yellow Perch from the western Lake Erie that ate a higher proportion of zooplankton were estimated to have higher

trophic positions than those which included more benthos in their diet.

Significant relationships between $\delta^{15}\text{N}$ and length were not likely a result of changes in carbon source with ontogeny, as no significant $\delta^{13}\text{C}$ - length relationships were found in either species. Increases in trophic position with size are very common in fish, and usually attributed to larger gape size and ability to feed on larger prey (Gatz, 1970; Zaret, 1980; Hobson and Welch, 1995; Anto and Turingan, 2010). However, size explained less than 42% of the variability and for many sites much less variability between $\delta^{15}\text{N}$ and length. While growth makes consumption of larger prey possible, the lack of variation explained by size suggests Yellow and White Perch of the sizes collected in this study are not utilizing fish as a primary food source. As a result, feeding by these species on primarily on zooplankton and benthos may limit increases in trophic position with growth.

The trophic niches, based on stable isotopes, indicated substantial niche overlap between Yellow and White Perch in the western basin of Lake Erie. The broader, more plastic diet of White Perch (Zuerlein, 1981; Stanley and Danie 1983; Couture and Watzin, 2008) was evident from their TA values, which were greater than those of Yellow Perch at all sampling locations. Interestingly, despite larger TAs, White Perch did not consistently have higher NR and CR values than Yellow Perch, suggesting complex spatial behaviours by these species. Yellow Perch CRs were larger than those of White Perch at Detroit plume, while White Perch had higher CRs at Maumee plume sites, again suggesting that resource utilization could be influenced by lake characteristics and prey availability. Increased consumption of zooplankton, which is known to have highly variable $\delta^{13}\text{C}$ values, by White Perch at Maumee plume and increased ability of Yellow Perch to capture benthos at Detroit plume, which is lower is zooplankton biomass and size (Legler, *unpublished*), may provide explanation for these differences in CR. No consistent

trends were evident in the NR of each species. While NR does provide insight into the vertical breadth of feeding by each species, it could alternatively be a bi-product of baseline variation or overall $\delta^{15}\text{N}$ availability amongst sites (Flaherty and Ben-David, 2010; Guzzo et al., 2010).

Relative distribution of niche areas on $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plots indicated high overlap of the trophic niches of Yellow Perch and White Perch in western Lake Erie. While these species differed in their feeding behaviors according to comparisons of their means, this high overlap indicated the potential for competition among these species if resources become limited (Schoener, 1974). High niche overlap has also been suggested to represent an absence of competition, indicating resources are in high abundance allowing species to share common resources (Brocksen et al., 1968; Schoner, 1974). The fact that Yellow Perch niche areas are typically bound within those of White Perch suggests that Yellow Perch lack any unique prey sources compared to White Perch, which may be disadvantageous to Yellow Perch if the species are forced to compete for limited resources in the system. This is particularly evident at Middle Sister Island where the entire niche area of Yellow Perch from being completely within that of White Perch. Alternatively, larger niche areas of White Perch could mean they are being outcompeted by Yellow Perch and are forced to exploit alternative resources. However, stable isotope analysis alone cannot provide definitive conclusions concerning the competitive interactions of these two species.

We also found large spatial differences in the NR and CR of zebra mussels between sampling locations. Since zebra mussels filter phytoplankton, this provides further evidence for spatial variation in isotope values of primary produces and lower trophic level organisms. These isotopic differences in primary consumers are known to be passed up the food chain to larger consumers (Kling et al., 1992; Kline et al, 1993; Cabana and Rasmussen, 1996). Therefore one

would predict site specific baseline differences in NR and CR ranges to be evident in zebra mussels and fish collected from the same location. For example, if Maumee River zebra mussels had the largest NR and CR of all sampling sites, fish from that plume would be expected to have largest NR and CR as well. This however was not supported by our results and can potentially be explained by movement of fish across sampling locations. Movement, and in turn foraging among multiple spatial zones, which are characterized by differences in nutrients and water characteristics would result in inconsistencies between NR and CR trends of zebra mussels and fish. While potential migration between plumes may inhibit our ability to assess site specific feeding behaviours it can also lead to increased food web stability through “soft-connections” as postulated by McCann et al., (1998).

Conclusion

In conclusion, stable isotope analysis of native Yellow Perch and non-native White Perch in the western basin of Lake Erie indicates that Yellow and White Perch are utilizing different food resources. High niche overlap suggests low levels of competition among the species, however, if food resources become limited White Perch may have a competitive advantage due to increased niche widths. Both species show an increase in trophic position but show no change in carbon sources with size, suggesting fish sampled in this study did not go through ontogeny. The results of this study suggest that niche width analysis with stable isotopes can be a valuable metric in assessing resource utilization and niche overlap of native and invasive aquatic species.

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1 Table 3.1 Stable isotopes, trophic position (TP) and length (mean \pm SE) of Yellow Perch, White
2 Perch and zebra mussels from four sites of the western basin of Lake Erie.

Site		Sample Type		
		Zebra mussel	Yellow Perch	White Perch
Maumee	<i>n</i>	12	32	30
	$\delta^{13}\text{C}$	-25.3 ± 0.49	-22.4 ± 0.16	-22.9 ± 0.21
	$\delta^{15}\text{N}$	7.97 ± 0.22	13.1 ± 0.17	14.0 ± 0.11
	TP	-	3.51 ± 0.03	3.79 ± 0.05
	Length	-	15.5 ± 0.36	15.4 ± 0.47
	Length (min-max)	-	10.2 - 20.6	10.7 - 22.0
Bass	<i>n</i>	16	31	28
	$\delta^{13}\text{C}$	-25.0 ± 0.36	-22.0 ± 0.09	-22.7 ± 0.22
	$\delta^{15}\text{N}$	8.53 ± 0.34	13.6 ± 0.12	14.3 ± 0.11
	TP	-	3.49 ± 0.04	3.76 ± 0.03
	Length	-	15.8 ± 0.37	16.4 ± 0.61
	Length (min-max)	-	11.9 - 21.0	13.0 - 22.8
Detroit	<i>n</i>	12	23	23
	$\delta^{13}\text{C}$	-22.9 ± 0.13	-21.1 ± 0.22	-22.3 ± 0.18
	$\delta^{15}\text{N}$	6.65 ± 0.09	13.1 ± 0.12	14.3 ± 0.23
	TP	-	3.88 ± 0.04	4.24 ± 0.07
	Length	-	15.2 ± 0.62	17.8 ± 0.94
	Length (min-max)	-	9.90 - 22.8	11.5 - 26.0
MSI	<i>n</i>	14	21	29
	$\delta^{13}\text{C}$	-23.8 ± 0.43	-21.7 ± 0.20	-22.6 ± 0.14
	$\delta^{15}\text{N}$	6.37 ± 0.12	12.6 ± 0.16	13.7 ± 0.18
	TP	-	3.83 ± 0.05	4.14 ± 0.05
	Length	-	17.4 ± 0.56	16.1 ± 0.62
	Length (min-max)	-	14.3 - 24	8.80 - 22.9
Basin-wide	<i>N</i>	54	107	110
	$\delta^{13}\text{C}$	-24.3 ± 0.22	-21.9 ± 0.10	-22.6 ± 0.10
	$\delta^{15}\text{N}$	7.43 ± 0.17	13.1 ± 0.07	14.1 ± 0.09
	TP	-	3.65 ± 0.03	3.95 ± 0.03
	Length	-	15.9 ± 0.24	16.4 ± 0.33
	Length (min-max)	-	9.90 - 24.0	8.80 - 26.0

3 Table 3.2 MANOVA and ANOVA analyses to test difference among Yellow and White Perch at each sampling location using both
4 isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$)

MANOVA ($\delta^{13}\text{C}$ - $\delta^{15}\text{N}$)	DF	Pillai Trace	F	Num df	P
Species	1	0.311	47.04	2	<0.001
Site	3	0.245	9.744	6	<0.001
Species:site	3	0.026	0.914	6	0.485
Residuals	209				
ANOVA ($\delta^{13}\text{C}$)	DF	Sum Sq	Mean Sq	F-value	P
Species	1	32.47	32.47	37.18	<0.001
Site	3	24.94	8.312	9.517	<0.001
Species:site	3	2.639	0.880	1.007	0.391
Residuals	209	182.5	0.873		
ANOVA ($\delta^{15}\text{C}$)	DF	Sum Sq	Mean Sq	F-value	P
Species	1	45.40	45.40	71.49	<0.001
Site	3	18.91	6.303	9.924	<0.001
Species:site	3	1.988	0.663	1.043	0.374
Residuals	209	132.7	0.635		

5

6

7 Table 3.3 Tukey HSD (Tukey Honestly Significant Differences) tests contrasting $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between sites. “Diff” reflects
 8 difference between sites (i.e., Detroit-Bass reflects mean of Detroit minus the mean of Bass).

$\delta^{13}\text{C}$	Diff	Lwr	Upr	P
Detroit-Bass	0.63	0.11	1.14	0.01*
Maumee-Bass	-0.30	-0.78	0.18	0.36
MSI-Bass	0.16	-0.35	0.66	0.85
Maumee-Detroit	-0.93	-1.44	-0.42	<0.001*
MSI-Detroit	-0.47	-1.00	0.07	0.11
MSI-Maumee	0.46	-0.04	0.96	0.08
$\delta^{15}\text{N}$	Diff	Lwr	Upr	P
Detroit-Bass	-0.27	-0.75	0.20	0.44
Maumee-Bass	-0.38	-0.82	0.180.06	0.11
MSI-Bass	-0.73	-1.19	-0.27	<0.001*
Maumee-Detroit	-0.11	-0.58	0.36	0.93
MSI-Detroit	-0.46	-0.95	0.03	0.08
MSI-Maumee	-0.35	-0.81	0.11	0.20

9 Table 3.4 Trophic niche metrics estimated for Yellow perch, White Perch and zebra mussels at
 10 each sampling location based on Layman et al. (2007), see methods for details. *NR* nitrogen
 11 range, *CR* carbon range, *TA* total area.

Site		Species		
		Yellow Perch	White Perch	Zebra mussel
Maumee Plume	NR	2.98	3.99	2.16
	CR	4.39	4.87	4.49
	TA	6.92	12.44	-
Bass Islands	NR	2.34	2.24	3.52
	CR	2.36	4.53	4.63
	TA	3.11	5.82	-
Detroit Plume	NR	2.88	4.64	0.85
	CR	5.44	3.58	1.32
	TA	5.77	7.72	-
Middle Sister Island	NR	2.52	3.98	1.42
	CR	2.72	2.98	5.27
	TA	1.90	7.53	-

Figure Legends

- Fig. 3.1 Populations estimate of adult (age 2+) Yellow Perch (white squares) and White Perch (black circles) in the western basin of Lake Erie from 1978 through 2009 (Matthew Norton, *unpublished data*; OMNR, *unpublished data*)
- Fig. 3.2 Location of sampling sites in the western basin of Lake Erie, sampled during June-September 2009. A= Maumee River Plume, B= Bass Islands, C= Detroit River Plume, D= Middle Sister Island.
- Fig. 3.3 Relationships between $\delta^{15}\text{N}$ versus length for Yellow Perch (triangles) and White Perch (circles) across four sampling sites in the western basin of Lake Erie. Dashed and solid lines are linear regression for White and Yellow perch, respectively. Equations, R^2 and P-values are presented only where significant regression were significant (α 0.05). Graph A= Maumee River Plume, B= Bass Islands, C=Detroit River Plume, D= Middle Sister Island.
- Fig. 3.4 Boxplots showing the interquartile range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of White Perch and Yellow Perch by site.
- Fig. 3.5 Bi-plot showing the mean ($\pm 95\%$ CI) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values averages for both species for each sampling location. Species were found to be significantly different at all sampling locations ($\alpha = 0.05$).
- Fig. 3.6 Trophic niches of Yellow Perch and White Perch collected May-September, 2009. Each symbol represents an individual fish of the two species. Polygons represent the total niche area occupied by each species. The thin line enclosing triangles represents Yellow Perch and the thick line enclosing circles represents White Perch. Graph A= Maumee River Plume, B= Bass Islands, C=Detroit River Plume, D= Middle Sister Island.

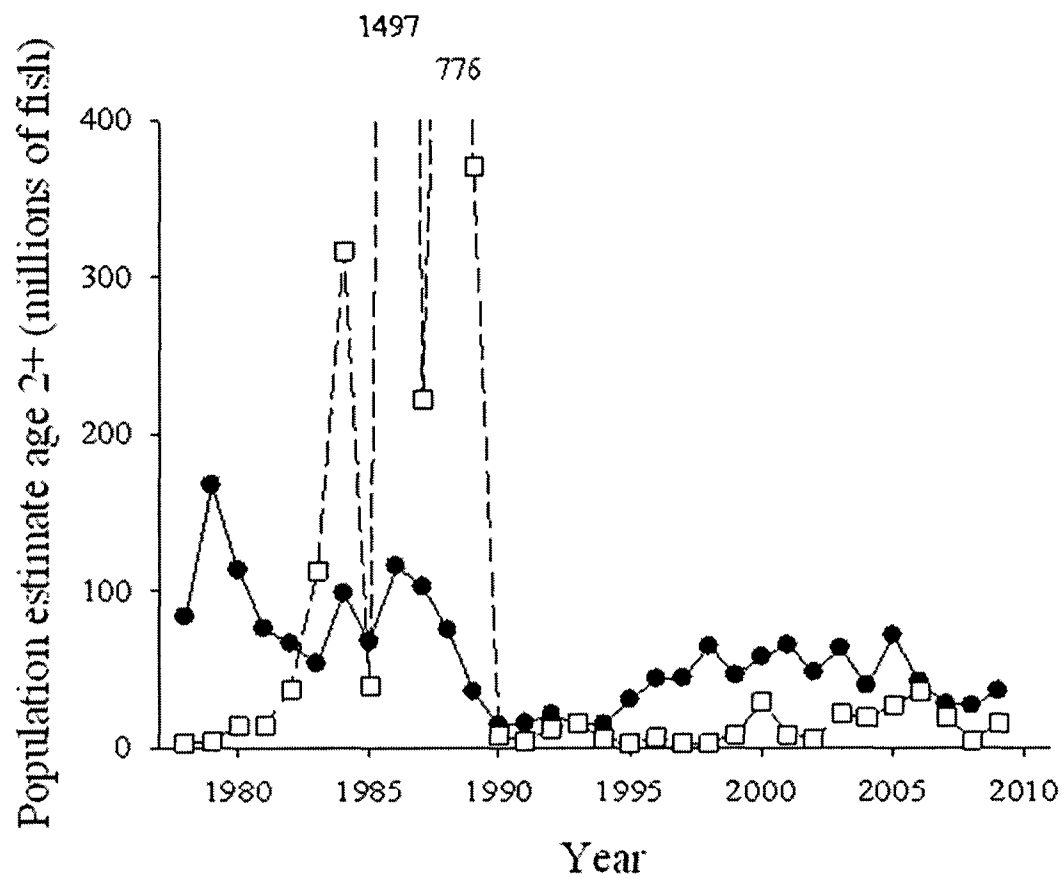


Figure. 3.1 Populations estimate of adult (age 2+) Yellow Perch (white squares) and White Perch (black circles) in the western basin of Lake Erie from 1978 through 2009 (Matthew Norton, *unpublished data*; OMNR, *unpublished data*)

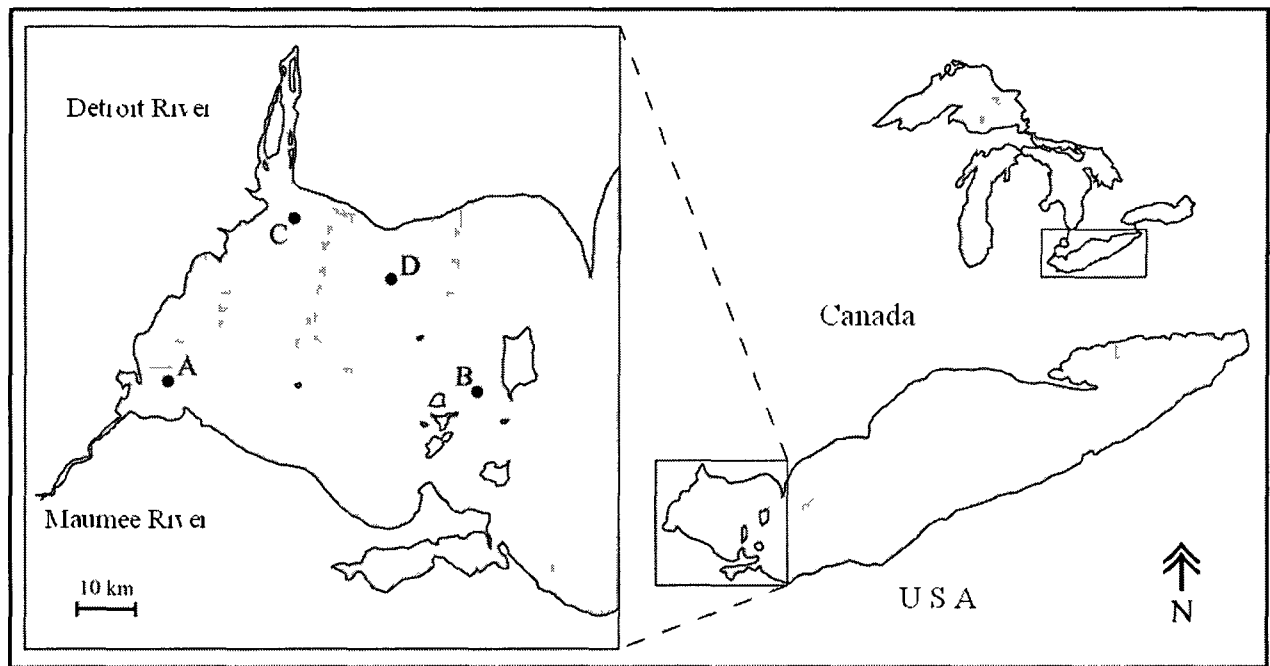


Figure 3.2 Location of sampling sites in the western basin of Lake Erie, sampled during June-September 2009. A= Maumee River Plume, B= Bass Islands, C= Detroit River Plume, D= Middle Sister Island.

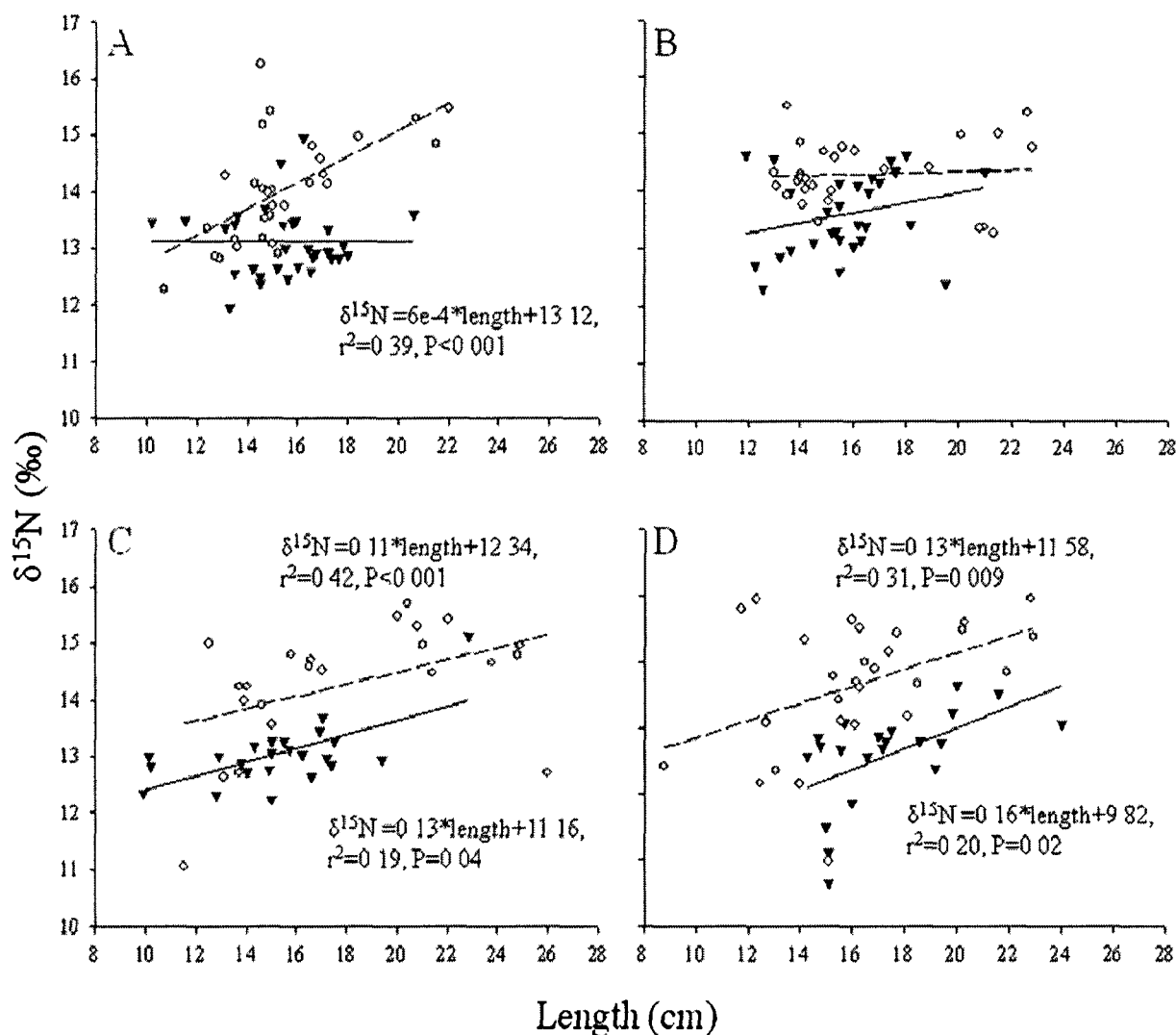


Figure. 3.3 Relationships between $\delta^{15}\text{N}$ versus length for Yellow Perch (triangles) and White Perch (circles) across four sampling sites in the western basin of Lake Erie. Dashed and solid lines are linear regression for White and Yellow perch, respectively. Equations, R^2 and P-values are presented only where significant regression were significant ($\alpha 0.05$). Graph A= Maumee River Plume, B= Bass Islands, C=Detroit River Plume, D= Middle Sister Island.

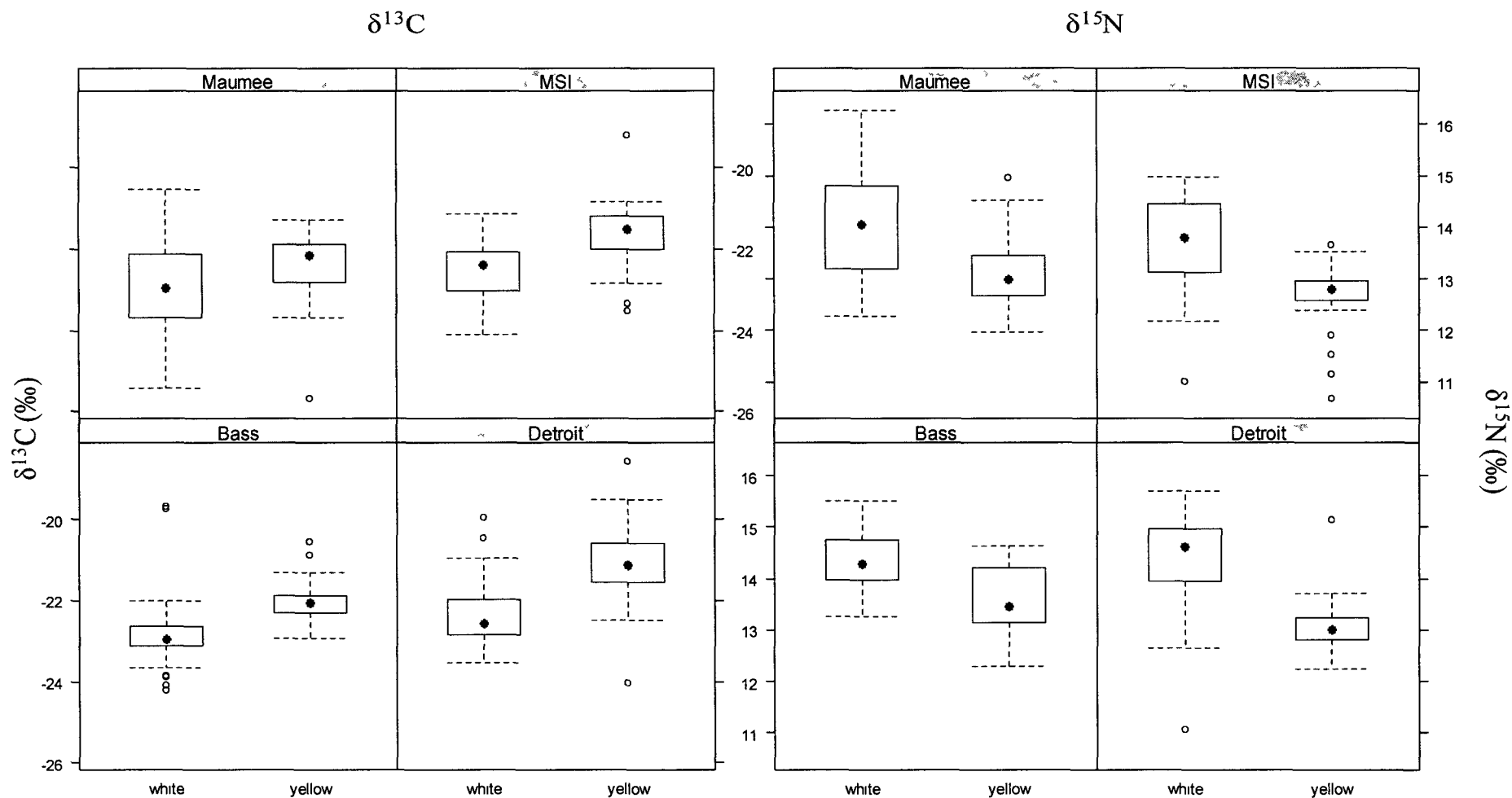


Figure 3.4 Boxplots showing the interquartile range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of White Perch and Yellow Perch by site.

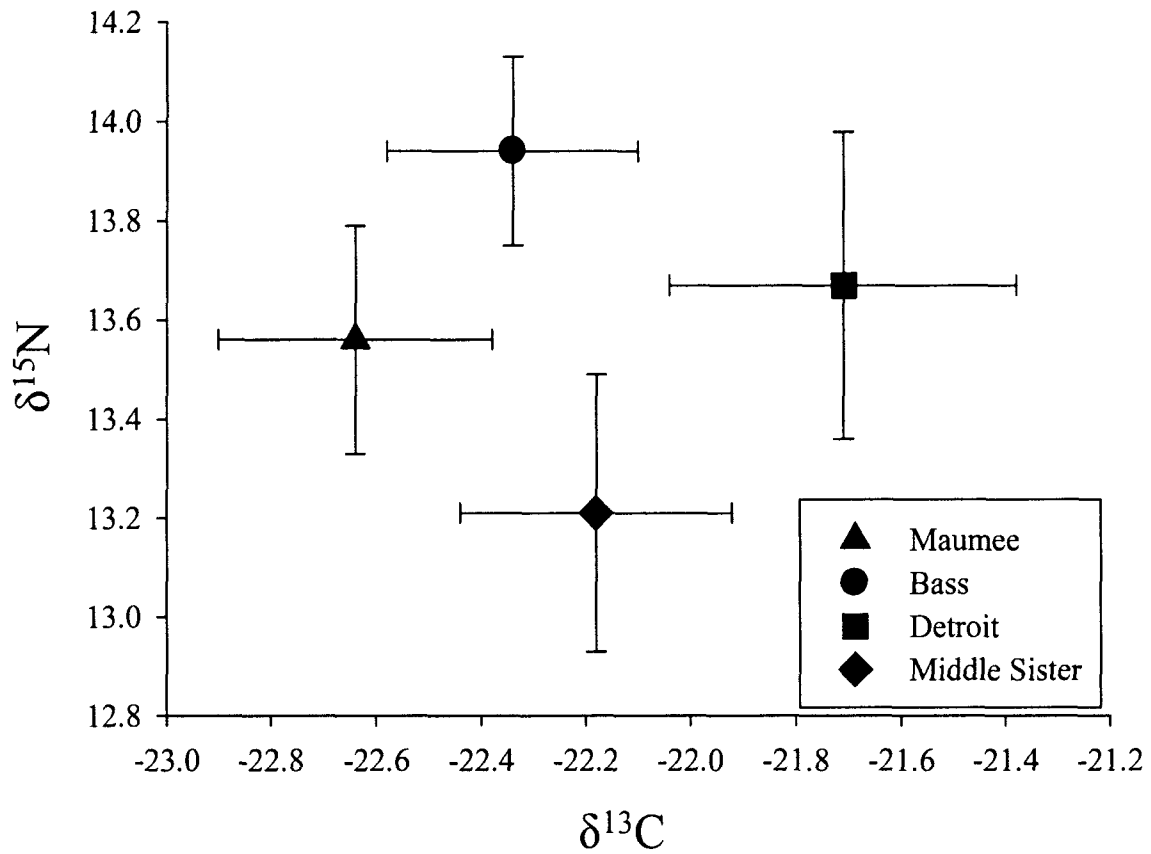


Figure 3.5 Bi-plot showing the mean ($\pm 95\%$ CI) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values averages for both species for each sampling location.

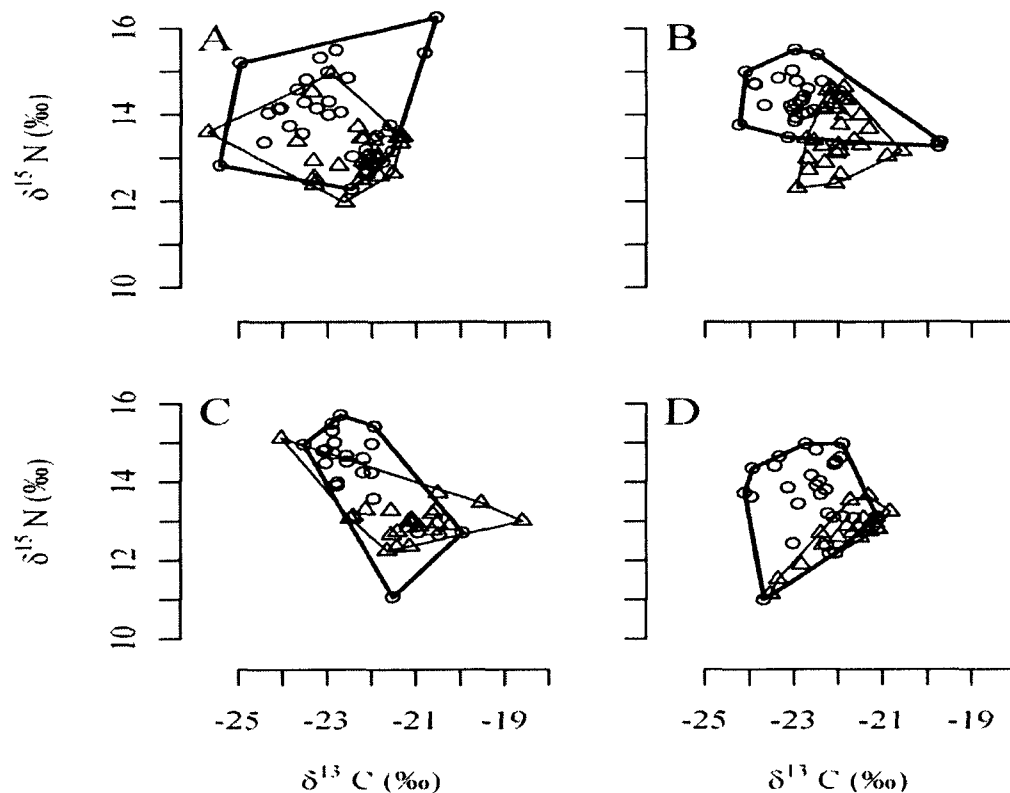


Figure 3.6 Trophic niches of Yellow Perch and White Perch collected May-September, 2009. Each symbol represents an individual fish of the two species. Polygons represent the total niche area occupied by each species. The thin line enclosing triangles represents Yellow Perch and the thick line enclosing circles represents White Perch. Graph A= Maumee River Plume, B= Bass Islands, C=Detroit River Plume, D= Middle Sister Island.

CHAPTER 4

CONCLUSION

Thesis Summary

The overall goal of this work was to examine the trophic ecology and niche overlap of Yellow Perch (*Perca flavescens*) and White Perch (*Morone americana*) across the spatially and temporally complex western basin of Lake Erie using stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$).

Chapter two evaluated the extent of spatial and temporal variability of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among lower trophic level species and its effects on estimating trophic position of consumers. This research was necessary to understand the spatial and temporal variability of stable isotopes in the western basin of Lake Erie in order to help in the interpretation of the results in chapter 3, which was the main objective of this thesis. By comparing isotope values of seston, zebra mussels (*Dreissena polymorpha*) and young-of-year Yellow and White Perch, several conclusions were reached. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of lower trophic level species can vary significantly spatially and temporally (months) across the same habitat zone of large lakes. Spatial variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, was a result of differences in physical and biological characteristics among sampling locations, while temporal differences were attributed to growth of young-of-year fish, increased zooplankton abundance and loss of spring terrestrial carbon influence to the lake. Temporal variation was found to explain the majority of stable isotope variation, however spatial effects accounted for the largest discrepancies in trophic position calculations of consumers.

The results of chapter two suggest that we must recognize the importance of stable isotopes variability in lower trophic level organisms in large lake systems, especially as stable isotopes continues to move from qualitative to more quantitative measures of trophic structure.

This is of particular importance when using lower trophic level organisms as baseline for assessing higher trophic level organisms using stable isotope. Our findings revealed that using baselines collected from non-corresponding sites or months when estimating trophic position could lead to variations up to 0.7 of a trophic level for secondary consumers, and potential more for higher consumers. This degree of error could have implications for fisheries management techniques, especially those that are based on mean catch trophic level values, as indicated by Branch et al., (2010).

Chapter three compared the relative carbon sources and potential niche overlap of adult yellow and white perch using stable isotopes and novel trophic niche metrics that use variation among individual isotope values; thus, at a basic level, providing need information on the trophic ecology of these species in the western basin of Lake Erie.. These values to compare the niche width and overlap were based on nitrogen range (NR), carbon range (CR) and total niche area (TA) of adult Yellow Perch and White Perch, where NR provides insight into feeding behavior and nitrogen sources and CR describes the breadth of food sources being consumed. TA represents the total niche area and is calculated from the convex hull area in the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plot (Layman et al. 2007). Differences in $\delta^{13}\text{C}$ among species indicated Yellow Perch's greater reliance on benthic food sources relative to White Perch. White Perch occupied a higher trophic position than Yellow Perch across the same size ranges. Trophic position, based on $\delta^{15}\text{N}$, was found to be positively correlated to size in both Yellow and White Perch. There was substantial niche overlap among Yellow and White Perch, based on stable isotopes, however differences in mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicated Yellow and White Perch are utilizing different food sources, but may have the potential to compete if resources become limited. White Perch had largest niche areas, consistent with its broad, plastic diet. These larger niches often full enclosed those of

Yellow Perch, suggesting Yellow Perch lack unique food sources from those of White Perch.

The relative feeding ecology of these two species varied with sampling location, suggesting that different nutrients and prey availability may influence the relationship between these species.

There are three major conclusions of this work:

1. Stable isotopes of lower trophic level species are susceptible to spatial and temporal variability which can inhibit our ability to accurately assess carbon source and calculate trophic position of consumers.
2. Stable isotopes provide a robust method for evaluating carbon sources and niche overlap of native and invasive fish species.
3. Yellow and White Perch are utilizing different forage bases and diet items, however high niche overlap indicated potential for competition if resources become limited in the western basin of Lake Erie.

Implications

Chapter 2

As the use of stable isotopes in aquatic systems continues to progress to more quantitative measures of trophic structure and interactions there must be a solid understanding of the causes and implications of stable isotope variability, particularly those in lower trophic levels which act as a forage base for consumers. Low trophic level species are also often used to baseline trophic position calculations and for estimating carbon sources for consumers (Post, 2002) and without understanding of their variability false conclusions could be made regarding food web structure and interactions (Guzzo et al., 2010). My finding of a 0.7 variation in trophic position when using different zebra mussels (from incorrect sites or months) has substantial implications for fisheries techniques that are based on mean catch trophic level. This was recently highlighted by

Branch et al., (2010) who indicated that benchmark work by Pauly et al., (1998), which concluded that that fisheries catches were decreasing in mean catch trophic levels over time was actually erroneous. The database that Pauly et al., (1998) used increased the trophic level estimate for anchoveta species by 0.5, substantially decreasing the mean catch trophic level trends and highlighting the sensitivity of this fisheries biomass estimate to uncertainties in trophic level estimates.

The results of this study also highlight the need to standardize sampling protocol for stable isotope analysis dependant on the species, size and lifespan of organisms being examined as these factors can lead to large difference in isotopic turnover (Perga and Gerdeaux, 2005). This will allow food web studies to capture key diet shifts and changes in habitat use in species with high turnover while saving time and money in collection of species in which isotope turnover occurs over the period of several months.

Chapter 3

In recent years there has been a call for ecosystem-scale fisheries management (GLFC, 2008). Traditional fisheries management techniques are often based on single species and fail to integrate trophic interactions among species and their ecosystems, both of which can affect the health of fish populations. Integration of invasive species into native food webs represent a mechanism by which trophic interactions may be altered, however, they are not accounted for by single species management techniques. In the western basin of Lake Erie, native Yellow Perch and invasive White Perch represent a high percentage of both recreational and commercial fish catches. In spite of this, very little is known about the trophic relationships among these two species. Understanding the interactions among these two species will enable lake managers to

predict how changes in fish abundance, nutrient dynamics and other large scale ecosystem changes might influence fish production and recruitment in the western basin of Lake Erie.

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VITA AUCTORIS

Matthew Guzzo was born in 1986 in Sault Ste. Marie, Ontario, Canada. He graduated from St. Mary's College in 2004 and went on to obtain a B.Sc. in Biology and Environmental Science in 2008. He is currently a candidate for the M.Sc. degree in Environmental Science at the Great Lakes Institute for Environmental Research, University of Windsor, Windsor, Ontario, Canada.